

Morphological Signatures of High-Altitude Adaptations in the Andean Archaeological Record: Distinguishing Developmental Plasticity and Natural Selection

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ABSTRACT

High-altitude hypoxia is one of many environmental stressors affecting human populations in the highland Andes. Living highland Andeans show adaptive physiological responses to these conditions through both developmental plasticity and natural selection. Given the longevity of human settlement in this region, these same responses ought to have affected ancient Andeans. This paper tests whether developmental plasticity or natural selection best explains the morphological signatures of adaptations to high-altitude hypoxia in ancient highland Andeans. I compare four groups of skeletons: two groups from lowland regions and two groups from high elevations. Previous work shows that the two highland groups have small bodies and voluminous ribs compared with the lowland groups indicating morphological adaptations to high-altitude environments. This paper compares patterns of intrinsic variation and sexual dimorphism in body size, limb lengths, and rib morphology in highland and lowland groups to test if developmental plasticity or natural selection underlies these morphological differences. The four groups share similar patterns of sexual dimorphism and intrinsic variation in body size and limb lengths. The two highland samples show greater degrees of sexual dimorphism in rib morphology than the lowlanders. Patterns of intrinsic variation in rib morphology do not sort by altitude. Both natural selection and developmental plasticity in response to high-altitude hypoxia likely shaped skeletal morphology in ancient highland Andeans.

Keywords:

Andes; high-altitude hypoxia; body size; rib morphology; developmental plasticity; natural selection

1. INTRODUCTION

This paper explores the evolutionary processes that underlie biological adaptations to high-altitude environments in the Andean archaeological record. With elevations that reach over 5,000 meters, high-altitude regions in the Andes present numerous environmental challenges to human populations that dwell there. These challenges include high-altitude hypoxia, limited nutritional availability, cold climates, high levels of solar radiation, and steep terrain. Despite these challenges, human populations have thrived in the highland Andes for millennia. Humans first settled at high altitudes at the end of the Pleistocene epoch (e.g., Aldenderfer, 1999; Aldenderfer and Flores Blanco, 2011; Rademaker *et al.*, 2014). Genetic and morphological data indicate that the initial inhabitants of the Andes shared similar origins with other early inhabitants of South America (Tarazona-Santos *et al.*, 2001; Fuselli *et al.*, 2003; Moraga *et al.*, 2005; Lewis *et al.*, 2007; Lewis and Long, 2008; Rothhammer and Dillehay, 2009; Hubbe *et al.*, 2011; Scliar *et al.*, 2012). The rich Andean archaeological record demonstrates continuous population growth, sociopolitical and economic interactions across vast geographic regions, and the rise of complex societies from the late Pleistocene to historic times (e.g., Moseley, 2001). Archaeological data also show that human populations thrived at high altitudes through agropastoral subsistence strategies, natural resource extraction, and long distance trade (Moseley, 2001).

Understanding the evolutionary processes that enabled humans to initially settle and subsequently thrive in the highland Andes is important given the physical challenges of living in this environment. Decades of research among living Andeans and other indigenous highland groups demonstrate many physiological and anatomical traits that enable humans

to successfully inhabit high-altitude regions (e.g., Beall, 2013; Frisancho, 2013; Little *et al.*, 2013). Cardiovascular and respiratory traits that enhance oxygen delivery under hypoxic conditions characterize many highland populations. These traits arise through developmental plasticity, in which adaptive traits emerge over the course of an individual's lifetime, and natural selection over many generations. Physical conditions that affect the biology of living populations also must have affected past groups that endured similar conditions. In order for humans to successfully thrive at high altitudes, biological adaptations to these conditions must have emerged early in the history of human settlement in the Andes. Many of the biological adaptations that function to alleviate high-altitude hypoxia and other stressors characteristic of high-altitude environments are identifiable in archaeological human skeletal remains (Weinstein, 2005, 2007, 2014). In particular, skeletons from the highland Andes exhibit longer and less curved ribs that indicate enlarged thoracic cavities synonymous with respiratory adaptations to high-altitude hypoxia. This paper tests whether these morphological patterns that characterize ancient Andeans arise through natural selection over many generations or developmental plasticity within a single generation.

1.1. Biological responses to environmental stress

The human body adjusts to environmental conditions via many biological processes that emerge across the life cycle and generations. Decades of research show that humans have successfully adjusted to the physical challenges of living at high altitudes through acclimatization, developmental plasticity, and natural selection. Acclimatization, the most immediate response to environmental stress, is the process in which the body rapidly

achieves homeostasis through adjustments to blood flow, ventilation, and other physiological functions (e.g., Frisancho, 1993, 2013). Developmental plasticity is a longer-term process in which an individual adjusts to environmental conditions over time through growth and maturation (Frisancho 1993, 2013; West-Eberhard, 2003). Natural selection is the evolutionary force in which, over many generations, specific genotypes and phenotypes confer a survival and reproductive advantage in specific environments. Long-term biological responses to high-altitude environments in living and ancient populations involve both developmental plasticity and natural selection. Yet each process shapes biological variation within a population differently. In order to distinguish developmental plasticity from natural selection in archaeological human skeletal remains, it is important to understand specific ways each process shapes morphological variation.

1.1.1. Developmental plasticity

Developmental plasticity occurs when individuals adjust to environmental conditions during the course of growth and development (Frisancho, 1993, 2013). Growth and maturation in harsh environmental conditions shape adult phenotypes (Kuzawa and Bragg, 2012). Individuals respond to their environments as they grow from juveniles to adults and their offspring also develop similar phenotypes during growth under the same conditions (West-Eberhard, 2003). Developmental plasticity is a longer-term response to environmental stress than acclimatization allows and a shorter-term response than the generational genetic changes required of natural selection (West-Eberhard, 2003; Kuzawa and Bragg, 2012). Developmental plasticity can minimize intrinsic phenotypic variation in a population quickly, potentially in one generation. (West-Eberhard, 2003; Pigliucci, 2001).

Life history theory explains how developmental plasticity works to shape adult variation in body size and sexual dimorphism (Kuzawa, 2007; Kuzawa and Bragg, 2012). Males and females utilize energy for growth and development differently. Females, based on hormonally driven physiological processes, require abundant and regular nutritional energy to maintain pregnancy and lactation. Females meet these reproductive demands through energy storage via body fat. In resource scarce environments, they respond through alterations to maturation rates leading to small adult body sizes (Kuzawa, 2007; Wells, 2012). Males, in contrast, are more labile and utilize excess energy to build fat-free body mass. Males can endure resource scarcity through growth faltering and reductions in adult body sizes. In harsh environments, reduced intrinsic variation in adult body size and sexual dimorphism within a population emerge from these developmentally plastic sex-specific growth patterns (Kuzawa and Bragg, 2012).

Recent work in paleoanthropology and human biology posit developmental plasticity as key for the modern human capacity to adapt to diverse environments, an ability that has enabled *Homo sapiens* to inhabit nearly every terrestrial ecosystem on earth (e.g., Antón and Snodgrass, 2012; Bribiescas *et al.*, 2012; Kuzawa and Bragg, 2012; Wells, 2012; Antón *et al.*, 2016). Developmental plasticity can set the stage for natural selection to occur within a population. Adaptations shaped by natural selection require many generations over thousands of years to become established within human populations (Kuzawa and Bragg, 2012). Yet as a species with expansive geographic ranges and long life histories, modern humans must adapt to varied environmental challenges at faster temporal rates than allowed by natural selection (Pigliucci, 2001; West-Eberhard, 2003; Kuzawa and Bragg, 2012). Developmentally plastic phenotypic variation can precede

genetic adaptation via natural selection in many human populations (West-Eberhard, 2003; Bribiescas *et al.*, 2012; Kuzawa and Bragg, 2012). Adult phenotypic variation then undergoes natural selection over many generations and thousands of years to gradually become genetically suited for that environment.

1.1.2. Natural selection

Adaptations via natural selection involve changes to underlying DNA sequences over many generations. Specific alleles and haplotypes that provide individuals with a reproductive advantage in a specific environment are the most direct evidence of natural selection. Beall (2007a,b, 2013), however, argues that anatomical and physiological traits with a large range of variation within a population are indicative of an underlying genetic adaptation in individuals with these traits. Variations in body size and body proportions, for example, can arise through natural selection to specific environmental conditions. Populations from cold climates tend to be heavier with shorter limbs while groups from warm climates tend to be thinner and taller with longer limbs, patterns that emerge over many generations (e.g., Ruff, 1994, 2002).

Sexual dimorphism in body size can also be shaped by natural selection. It operates either via sexual selection, which increases access to mates, or via sex differences in response to local environmental conditions (Plavcan, 2012). In humans, the soft tissue and skeletal components of the thorax show sexual dimorphism in ways that reflect differences in energy demands between males and females (Bellemare *et al.*, 2003, 2006; Froehle and Churchill, 2009; Shi *et al.*, 2014; Weaver *et al.*, 2014; García-Martínez *et al.*, 2016).

Compared with most other primate species that are highly dimorphic, sexual dimorphism

in modern humans is moderate and fluctuates around 12-15%. Within this range, human populations vary in sexual dimorphism based on resource availability and latitude (Plavcan, 2012). Among closely related and geographically proximate human groups, genetic factors do not explain much of the variation in sexual dimorphism (Kuzawa and Bragg, 2012; Plavcan, 2012). Thus, populations enduring natural selection to environmental stress should exhibit high levels of intrinsic variation and moderate degrees of sexual dimorphism in body size and body proportions when compared with groups that are not exposed to this environmental stress.

1.2. High-altitude hypoxia: developmental plasticity and natural selection.

High-altitude hypoxia arises when bodily tissues receive an insufficient supply of oxygen as a result of the reduced barometric pressure of atmospheric oxygen. At sea level, the barometric pressure of atmospheric oxygen is 100% and progressively decreases with increasing altitude. The adverse effects of high-altitude hypoxia physiologically take effect at 2,500 m at rest and at 2,000 m during physically strenuous activity (Frisancho, 1993). High-altitude hypoxia is chronic, and unlike other environmental stressors, cannot be alleviated through changes in behavior or cultural technology.

Many physiological traits function to enhance oxygen transport to bodily tissues in response to high-altitude hypoxia. These traits include increases in red blood cell production, hemoglobin concentration, ventilation, lung volumes at all phases of inspiration and expiration, and oxygen saturation of arterial hemoglobin (e.g., Frisancho, 1993; 2013). The human body immediately physiologically adjusts to high-altitude hypoxia within minutes through weeks of exposure through the process of acclimatization

(Frisancho, 1993, 2013). All individuals, regardless of ancestry, are capable of acclimatizing to high-altitude hypoxia. Given a long enough period at high elevations, most individuals will show enhanced oxygen transport traits that function to reduce the adverse effects of high-altitude hypoxia (Frisancho, 2013).

Despite the universal ability to acclimatize to high-altitude hypoxia, human populations permanently living at high altitudes exhibit more efficient oxygen transport traits than newcomers to altitude (e.g., Greksa, 1990; Brutsaert, 2010; Beall, 2013). Indigenous highland populations from the Andes and Himalayas have lower pulmonary ventilation rates, larger lung volumes, higher red blood cell counts, elevated hemoglobin concentrations, and increased oxygen saturation of arterial hemoglobin compared with lowland groups and adult migrants to high altitudes (e.g., Frisancho *et al.*, 1973, 1995, 1997, 1999; Greksa and Beall, 1989; Beall *et al.*, 1997; Curran *et al.*, 1998; Brutsaert *et al.*, 1999a, 1999b, 2004; Garruto *et al.*, 2003; Beall, 2006; Brutsaert, 2010; Kiyamu *et al.*, 2012). Enlarged chests relative to stature and body mass also characterize indigenous highland groups compared with closely related lowlanders and high-altitude migrants (e.g., Frisancho *et al.*, 1973; Beall *et al.*, 1977; Beall, 1981; Eckhardt, 1985; Greksa and Beall, 1989; Kramer, 1992; Brutsaert *et al.*, 1999a; Weitz *et al.*, 2004; Brutsaert, 2010).

Developmental plasticity has been an important explanation of biological adaptations to high-altitude environments in living Andean populations. Human biologists researching high-altitude adaptations in indigenous highland Andeans in the 1960s and 1970s initially hypothesized that high-altitude hypoxia was the primary cause of delayed childhood growth and short adult stature observed in these groups (e.g., Frisancho and Baker, 1970; Little *et al.*, 2013). Later work, however, revealed that nutritional stress

during childhood associated with poor socioeconomic conditions more adequately explained the delayed growth patterns and small adult body sizes in many indigenous highland Andeans (Stinson, 1980, 1982, 1990 2009; Greksa *et al.*, 1984, 1985; Greksa, 1986; Leonard, 1989; Leonard *et al.*, 1990, 1995, 2000; Katzmarzyk and Leonard, 1998; Pawson *et al.*, 2001; Leonard and Katzmarzyk, 2010; Pawson and Huicho, 2010; Little *et al.*, 2013).

Nevertheless, Paul Baker and colleagues working with indigenous highland groups in Nuñoa, Peru beginning in the 1960s posited that developmental plasticity explained the enhanced oxygen transport traits in response to chronic hypoxic conditions (e.g., Frisancho, *et al.*, 1973, Frisancho, 2013; Little *et al.*, 2013). Later research among indigenous highland groups in the Andes, Africa, and Asia further corroborated developmental plasticity as the primary explanation of enhanced oxygen transport traits (e.g., Greksa and Beall, 1989; Greksa, 1990; Garruto *et al.*, 2003; Frisancho, 2013).

Individuals born and raised at high altitudes regardless of ancestry develop oxygen transport traits to a greater degree than individuals who migrate there as adults. The altitudinal environment in which an individual was born and matured forms the basis for establishing adult physiological function. The earlier an individual experiences chronic high-altitude hypoxia, the fitter and more functionally adapted that individual will be to high-altitude conditions (Frisancho, 1993, 2013). European children raised in highland Peru and Bolivia and Han Chinese children raised at high altitudes in China develop enlarged lung volumes that resemble those of native highland populations (Greksa *et al.*, 1985; Frisancho and Greksa, 1989; Greksa and Beall, 1989; Frisancho *et al.*, 1997; Brutsaert *et al.*, 1999a,b, 2004; Weitz *et al.*, 2002, 2013; Brutsaert, 2010). Similarly, lowland

individuals who moved to highland regions as young children develop enhanced aerobic capacities that approximate those of indigenous highlanders (Frisancho and Greksa, 1989; Frisancho *et al.* 1995; Brutsaert *et al.*, 1999b; Brutsaert, 2010). Differences in lung volumes in indigenous highland Andean populations compared with their lowland neighbors, moreover, are established by 10-12 years of age (Burri, 2006; Calogero and Sly, 2010; Frisancho, 2013).

Recent research in genetic variation indicates that natural selection also underlies the enhanced oxygen transport functioning in indigenous highland populations (e.g., Beall *et al.*, 1998; 2004; Beall, 2006, 2007a, 2007b, 2013; Bigham *et al.*, 2008, 2013; Moore, 2016). Over the course of millennia indigenous highland Andeans, Tibetans, and Ethiopians have undergone natural selection for different pathways to achieve convergent adaptive responses to chronic high-altitude hypoxia. Highland Tibetans, for example, show phenotypic and genetic variances indicating that these populations have undergone natural selection for ventilation rates, hemoglobin concentration, oxygen saturation of arterial hemoglobin, and lung volumes (e.g., Beall *et al.*, 1998; 2004; Beall, 2006, 2013; Bigham *et al.*, 2008, 2013; Weitz *et al.*, 2016). Highland Amhara populations in Ethiopia show phenotypic and genetic variation indicating positive selection for elevated pulmonary arterial pressure and hemoglobin concentration in ways that differ from those of highland Himalayan and Andean populations (Hoit *et al.*, 2011; Scheinfeldt *et al.*, 2012).

Highland Aymara and Quechua populations have enlarged chests relative to stature, a morphological pattern associated with enhanced oxygen transport efficiency in response to high-altitude hypoxia (Beall *et al.*, 1977; Beall, 1981; Greksa and Beall, 1989; Frisancho *et al.*, 1997; Brutsaert *et al.*, 1999a, 2004). Highland Quechua groups from Peru have larger

chest for stature and develop these anatomical traits at earlier ages than highland Himalayan children (Beall, 1981; Greksa and Beall, 1989). Highland Aymara and Quechua also have larger degrees of phenotypic variance in chest size than highland Himalayan populations suggesting that this trait was shaped by natural selection in Andean populations (Eckhardt, 1985; Kramer, 1992; Williams-Blangero *et al.*, 1993). Enlarged thoracic cavities also characterize ancient highland Andeans based on longer and less curved ribs in human skeletons from highland archaeological sites compared with those from lowland regions (Weinstein, 2007, 2014). While the multitudes of data suggesting that the highland Andean pattern of enlarged chests and enhanced lung volumes arises through both developmental plasticity and natural selection, the exact biological processes that led to the emergence of these morphological traits in the archaeological record remain unclear.

1.3. Goals of this study

Studies of extant Andean populations show that both developmental plasticity and natural selection are important phenomena that explain the emergence of biological adaptations to high-altitude environments. Yet developmental plasticity and natural selection yield contrasting patterns of variation in body size, body proportions, and sexual dimorphism. Given that humans have occupied the highland Andes for millennia, the same processes that shape the biology of extant human groups also must have affected ancient populations. In order to distinguish developmental plasticity from natural selection to high-altitude environments in the Andean archaeological record, I compare four groups of skeletons from different elevations: two groups from high elevations and two groups from

lowland regions. Previous work shows that the highland groups exhibit small adult body sizes and longer ribs that encompass greater area with less curvature than their lowland counterparts in patterns that suggest respiratory adaptations to high-altitude hypoxia (Weinstein 2005, 2007, 2014). The exact processes – developmental plasticity or natural selection – that shaped these patterns have yet to be established.

One approach to distinguishing developmental plasticity from natural selection in skeletal morphological patterns of high-altitude adaptations involves analyzing intrinsic variation and sexual dimorphism. Developmentally plastic responses to environmentally induced resource scarcity ought to effect adult size in males more profoundly than in females due to sex differences in energy allocation during growth. If developmental plasticity best explains high-altitude adaptations, then body size and rib morphology in the highland groups should exhibit reduced levels of sexual dimorphism and lower levels of intrinsic variation in males compared with females. Alternatively, if natural selection to high-altitude environments best explains variations in body size and rib morphology, then males and females from high-altitude regions should show equal levels of intrinsic variation and normal to high levels of sexual dimorphism.

2. MATERIALS AND METHODS

2.1. Human Skeletal Samples

I compare four sex-specific samples of adult skeletons: two lowland (Arica, Chile and Ancón, Peru), and two highland groups (San Pedro de Atacama, Chile, and Machu Picchu and Cuzco, Peru) (Table 1). The archaeological context of each group is described in detail elsewhere (Weinstein 2005, 2007, 2014). The two lowland samples are from Pacific coastal

sites and consumed both marine and agricultural foodstuffs (Llagostera, 1989; Arriaza, 1995; Arriaza *et al.*, 1995; Standen *et al.*, 1997). The highland sample from San Pedro de Atacama, Chile, is from 2,500 m, an elevation that is high enough for the human body to experience the adverse effects of high-altitude hypoxia. Individuals from this group generally subsisted on camelid meat, maize, and tubers (Costa, 1988; Llagostera *et al.*, 1988; Neves and Costa, 1998; Neves *et al.*, 1999). The second highland sample is from Machu Picchu (2,000-2,850 m) and Cuzco (3,500-3,800 m) and consumed a diet high in maize (Burger and Salazar, 2003; Burger *et al.*, 2003). While these four samples largely overlap temporally (Table 1), previous work shows that morphology does not vary by temporal divisions (Weinstein, 2001).

2.2. Osteometric variables and statistical analysis

I measured maximum lengths of the humerus, radius, femur, and tibia with a Paleotech osteometric board and the antero-posterior diameter of the femoral head with Mitutoyo digital calipers. I estimated body mass in kg using the average of three published regression equations based on the relationship between the femoral head diameter and body weight (Ruff *et al.*, 1991; McHenry, 1992; Grine *et al.*, 1995). I also measured rib area, the area encompassed within each rib, for ribs 1-9 based on the equation defined by Franciscus and Churchill (2002). I did not measure this variable for ribs 10-12 because of missing data for rib 10 and lack of a tubercle in ribs 11-12. I explain the definitions of these osteometric variables elsewhere (Weinstein 2005, 2007, 2014).

If biological adaptations to high-altitude environments result from developmental plasticity, then skeletons should demonstrate responses to resource scarcity in the same

developmentally induced patterns documented for living humans. Developmentally plastic responses to resource scarcity include two patterns. First, highland males should exhibit low levels of intrinsic variation compared with females for a given trait if this trait has emerged through developmental plasticity. Second, there should be low levels of sexual dimorphism with a particular reduction in male size in highland groups compared with lowlanders. Alternatively, if natural selection is the most robust explanation for adaptations to high-altitude environments, then highland males and females should show equal levels of intrinsic variation and normal to high levels of sexual dimorphism compared with lowlanders.

I test whether sexual dimorphism differs between groups from different altitudes by calculating a sexual dimorphism index (SDI), computed as male mean/female mean, for all variables. I compare sex-specific mean values of all variables by site using two-tailed T-tests with unequal variance (Table 2) and Bonferroni comparisons to assess differences between groups in SDI (Table 3). I also compare intrinsic variation between males and females from the same site. While the coefficient of variation is commonly used to describe intrinsic variation in morphological variables within a group, it can be cumbersome to compare statistically between samples (Lewontin, 1966, Plavcan 2012). I follow Lewontin's (1966) recommendation to compare intrinsic variation by calculating the log-transformed variance of a morphological variable ($s^2_{\log x}$). I then compare levels of intrinsic variation between males and females from the same site by calculating the ratio of logged variance for each sex ($s^2_{\log x}/s^2_{\log y}$) against the F distribution table (Table 4) and illustrate significant differences between groups via Bonferroni comparisons (Table 5). This method has been used in other studies that compare intrinsic morphological variation in closely related

populations of modern humans, vervet monkeys, and macaques (Antón *et al.*, 2016). I also conduct nonparametric Levene's tests of logged transformed data for each variable as an alternative method to assess whether males and females from the same site have equal variances (Table 6). This test measures the absolute difference of each individual's ranked-order value of a specific trait from its mean and then calculates sex-specific differences via ANOVA (Plavcan and Cope, 2001; Van Valen, 2005; Nordstokke and Zumbo, 2010).

3. RESULTS

Previous work shows significant differences in body mass, limb lengths, and rib areas between the highland and lowland samples (Weinstein, 2005, 2007, 2014). The two highland samples have smaller body masses with longer limbs than the two lowland samples that are heavier with shorter limbs (Weinstein, 2005, 2014). Rib areas also distinguish the two highland samples from the two lowland groups. Both Atacama males and females have significantly larger rib areas at all levels of the thorax compared with the two lowland groups. Males from Machu Picchu/Cuzco also have large rib areas similar to the Atacama sample. Despite a small sample size for rib data (Table 2), Machu Picchu/Cuzco females show small rib areas at all levels of the thorax and resemble the thoracic morphology of females from the two lowland sites (Weinstein, 2007, 2014).

Sexual dimorphism indices range between 1.08 and 1.17 for body size and limb lengths and between 1.08 and 1.75 for rib areas (Table 2). Sexual dimorphism indices for body size and limbs lengths significantly differ within all four groups in magnitudes that approximate the 12-15% dimorphism characterizing modern human populations (Plavcan, 2012). Sexual dimorphism indices in rib areas, however, reveal a different pattern. Atacama

males and females significantly differ at all levels of the thorax. Machu Picchu/Cuzco males and females have highly dimorphic ribs with significant differences at ribs 4-6 and 8-9. The two lowland samples show much less sexual dimorphism in rib morphology. Arica males and females significantly differ from each other at ribs 6-8. Ancón males and females significantly differ in sexual dimorphism at rib four and rib nine, which is actually slightly larger in females than males.

Sexual dimorphism indices for body size and limbs lengths do not differ between groups (Table 3). Sexual dimorphism indices in rib areas, however, strongly differentiate highlanders from lowlanders. Machu Picchu/Cuzco individuals have significantly higher sexual dimorphism indices for all rib areas compared with the three other groups reflecting markedly large rib areas in Machu Picchu/Cuzco males compared with the especially small rib areas in Machu Picchu/Cuzco females. Sexual dimorphism indices in Atacama individuals are significantly larger than the two lowland groups for ribs 1-3 and 8-9.

Ratios of sex differences in intrinsic variation by site for body size and limb lengths range from 1.00 to 1.69, but none of these differences is statistically significant (Table 4). In most cases, males and females from the same site show equal or nearly equal intrinsic variation for body size and limb lengths. For rib morphology, males tend to show greater intrinsic variation compared with their female counterparts, but these differences rarely attain statistical significance (Table 4). Arica males have significantly larger intrinsic variation than females for ribs 4-5 and 8-9. Despite the lack of statistical significance, Machu Picchu and Cuzco highlanders tend to show the greatest degree of male/female differences in intrinsic variation, followed by Arica and Ancón lowlanders and San Pedro de Atacama highlanders with the smallest values of intrinsic variation in rib areas.

Comparisons of intrinsic variation by site show some notable patterns (Table 5). Machu Picchu/Cuzco individuals tend to have significantly greater intrinsic variation in body mass and limb lengths. Atacama highlanders and Arica lowlanders tend to have the least intrinsic variation for body mass and limb lengths. Intrinsic variation in rib areas also statistically differentiates these four groups, but not by consistent altitudinal patterns. In most cases, Atacama males and females have significantly lesser intrinsic variation in rib areas compared with at least one other group. Machu Picchu/Cuzco males and females show a highly variable pattern in intrinsic variation in rib morphology. In many cases, intrinsic variation in this group is significantly less than at least one lowland group. At ribs three, four, six, and eight, however, Machu Picchu/Cuzco highlanders show significantly greater sex differences in intrinsic variation compared with Atacama highlanders and at least one lowland group.

Nonparametric Levene's test results reveal a different pattern of intrinsic morphological variation between males and females from each site (Table 6). Machu Picchu/Cuzco males and females show no significant differences in intrinsic variation in body size, limb lengths or rib areas, although small sample sizes may influence these results. Atacama males and females, in contrast, show significant differences in intrinsic variation in all variables except for rib five, indicating that males have significantly greater variation in these morphological traits than females. Arica males similarly show significant greater intrinsic variation in body mass, limb lengths, and ribs 4-7 and rib 9 than their female counterparts. Ancón males show significantly greater intrinsic variation in body mass and limbs lengths compared with Ancón females, but do not differ from their female counterparts in intrinsic variation in rib areas.

4. DISCUSSION

Previous work shows that ancient Andean highlanders tend to have skeletal manifestations of lighter bodies, longer limbs, and more voluminous ribs than lowland Andeans. These patterns resemble those of living Andean populations and suggest adaptations to high-altitude environments (Weinstein, 2005, 2007, 2014). Yet patterns of intrinsic variation and sexual dimorphism in body size, limb lengths and rib morphology among these same skeletons suggest that there is no uniform biological response to hypoxia or other high-altitude environmental stressor. Males and females from each site, regardless of altitude, significantly differ from each other in sexual dimorphism in body mass and limb lengths in ways that adhere to normal patterns of sexual size dimorphism in modern humans (Plavcan, 2012). The two highland samples have more sexually dimorphic rib areas compared with the lowland groups. Atacama males and females show less intrinsic variation in rib morphology compared with lowlanders. Other than these observations, however, sex-specific patterns of intrinsic variation in rib morphology do not sort by altitude in consistent patterns

Patterns of variation in rib morphology do not point exclusively to either developmental plasticity or natural selection. Greater degrees of sexual dimorphism in rib areas in the highland groups compared with lowlanders suggest natural selection to high-altitude hypoxia. Yet the lack of a discernable pattern of intrinsic variation in rib areas does not rule out developmental plasticity as a factor. The lack of clarity in distinguishing developmental plasticity from natural selection in these skeletons is not surprising given the vast amount of research that demonstrates the work of both phenomena in shaping

thoracic morphology in living highland Andeans. Below I discuss the lack of clarity in distinguishing developmental plasticity and natural selection in skeletal indicators of adaptations to high-altitude hypoxia as well as other factors that may have influenced morphological variation in the ancient Andes.

Developmental plasticity has long been invoked as the biological process through which human populations become adapted to chronic high-altitude hypoxia (e.g., Frisancho, *et al.*, 1973; Frisancho, 1993, 2013; Little *et al.*, 2013). As a process that works across an individual's lifetime and most profoundly during the fetal period, infancy and childhood, it shapes adult phenotypes regardless of ancestry in any particular environment. It can give rise to physiological and anatomical traits in many individuals within a population in a single generation (West-Eberhard, 2003). Given the physical challenges of living at high altitudes and that adaptations via natural selection require generations to become common within a population, developmental plasticity must have played an important role in enabling the earliest populations to initially settle the highland Andes. Through developmental plasticity, the earliest highland Andeans must have grown enhanced lung volumes, enlarged thoracic cavities and other key physiological and anatomical traits that facilitate high-altitude living.

The role of natural selection acting on Andeans and other highland populations through time also cannot be dismissed. Indigenous highland populations from Asia, Africa, and South America differ in genetic traits that confer specific adaptive pathways towards enhanced oxygen-transport efficiency (e.g., Beall, 2007b, 2013; Moore, 2016). These differences suggest the work of natural selection acting on these populations independently in recent human evolutionary history (e.g., Beall, 2013; Bigham *et al.*, 2013).

What remains to be demonstrated is a clear link between specific genetic traits and phenotypes that provide enhanced physiological function and that are linked to the morphological patterns observed in living and ancient highland Andean peoples.

Body size and limb lengths show normal patterns of sexual dimorphism and no sex-specific pattern of intrinsic variation in ways that distinguish highland and lowland groups. These results suggest that developmental plasticity is not detectable in these specific measures of morphological variation in these samples. Yet previous work shows that body mass is significantly smaller in the two highland samples compared with the lowland groups (Weinstein 2005, 2014). While not specifically tested here, the smaller body sizes in the highlanders resemble the biological responses to limited nutritional energy observed in some living Andeans and strongly suggest the work of developmental plasticity.

Fluctuations in body size and proportions are notable in 20th-21st century Andean groups who endure impoverished socioeconomic conditions and poor diets (e.g., Stini, 1969, 1972, 1975; Leonard, 1989; Stinson, 2009; Leonard *et al.*, 1990, 1995, 2000; Pawson and Huicho, 2010; Little *et al.*, 2013; Pomeroy, *et al.* 2013; 2015). Diets and subsistence practices differ between highland and lowland Andeans in the archaeological record. Machu Picchu/Cuzco and Atacama highlanders consumed a typical highland Andean diet of maize, tubers, hardy grains, and camelid meat that seasonally fluctuated in quality and quantity and that varied by socioeconomic status (e.g., Costa, 1988; Costa Junquiera and Llagostera, 1994; Miller, 2003; Burger *et al.*, 2003; Hubbe *et al.*, 2012; Knudson *et al.*, 2015). The highland Andean agropastoral diet could have been less diverse in nutrient quality, especially seasonally, compared with the marine-based and agricultural diets of coastal groups. Diets lacking in food diversity can result in delayed growth and short adult stature (Leonard *et al.*, 1990;

Bogin, 1999). Future work on ecological and evolutionary factors shaping ancient Andean morphological variation should more directly address the effects of diet and energy availability.

While not specifically examined in this study, it is also important to recognize the role of gene flow in influencing morphology in ancient Andeans. Genetic variation among living and ancient Andeans indicates that gene flow between densely populated regions was ubiquitous through time (e.g., Tarazona-Santos *et al.*, 2001; Moraga *et al.*, 2005; Scliar *et al.*, 2012). Moore and Rademaker (2016) show that early highland groups in southern Peru transported natural resources across vast distances and altitudinal zones. Atacama populations show strong affinities to people from the highlands to the east as well as cultural and political ties with groups living at lower elevations (Knudson *et al.*, 2012; 2015; Torres Rouff *et al.*, 2013, 2015). Atacama populations also show diversification in ethnicity, socioeconomic status, and cultural practices over the last millennium (e.g., Torres-Rouff and Costa Junqueira, 2006; Torres-Rouff, 2011; Hubbe *et al.*, 2012; Torres Rouff *et al.*, 2013; 2015; Knudson *et al.*, 2015). Archaeologists have long maintained that Inca-period Machu Picchu and Cuzco residents originated from across the Andes based on the Inca practice of relocating entire ethnic groups as part of empire building (Moseley, 2001; Burger and Salazar, 2003). Gene flow across altitudinal zones was an important phenomenon that occurred with regularity in the Andean past and must have shaped morphological variation in ancient Andean populations. The regularity and ease at which individuals and populations moved across the landscape regardless of altitude suggests that developmentally plastic biological processes continuously affected individuals and groups throughout the history of human settlement in the Andes.

Distinguishing developmental plasticity from natural selection and other evolutionary forces in the archaeological record poses unique methodological challenges. Human biologists researching developmental plasticity and natural selection in extant populations commonly compare the physiology, anatomy, and genetic traits of contemporaneous living groups that differ in geography and ecological conditions or who comprise a longitudinal sample from one region. Yet this comparative, longitudinal, and temporal precision is rarely available to researchers working with ancient human skeletons. Given the importance of developmental plasticity and natural selection to the human biological capacity to settle in every terrestrial ecosystem on earth, including high-altitude environments, future work on human adaptations to environmental stress should incorporate innovative models for distinguishing these phenomena in the past. Interdisciplinary collaborations between archaeologists, biological anthropologists, and geneticists will further elucidate the processes that have enabled human populations to thrive for millennia at high altitudes.

5. CONCLUSION

Both developmental plasticity and natural selection are important phenomena that must have affected the biology of ancient highland Andeans. Patterns of sexual dimorphism in body size and limb lengths do not distinguish highland groups from their lowland counterparts. Patterns of intrinsic variation and sexual dimorphism in rib morphology suggest that highland groups responded to the chronic stress of high-altitude hypoxia through both developmental plasticity and natural selection in ways that resemble living Andeans. Developmental plasticity and natural selection are important evolutionary

processes to consider in explanations about the biological adaptations to high-altitude environments that must have emerged early in the Andean archaeological record.

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Table 1: Sample composition

Sample	Males	Females	Altitude (m)	Dates
Machu Picchu/ Cuzco, Peru	22	19	2000-3800	15 th century
San Pedro de Atacama, Chile	42	60	2500	250-1240 C.E.
Arica, Chile	54	69	<100	3210-1720 B.C.E. 750-1250 C.E.
Ancón, Peru	52	28	<100	1000-1476 C.E.

Table 2: Sexual dimorphism index (SDI), sample sizes, and mean values by sex. Significant differences between males and females are noted in bold ($P < 0.01$).

Sample	Machu Picchu/ Cuzco	San Pedro de Atacama	Arica	Ancón
Body mass (kg)				
SDI	1.17	1.16	1.13	1.17
Male mean	58.60	61.34	62.27	66.36
N	16	40	49	50
Female mean	49.96	52.74	55.13	56.83
N	12	53	68	27
Humerus length (mm)				
SDI	1.09	1.08	1.08	1.11
Male mean	293.79	301.17	299.10	298.96
N	14	39	46	52
Female mean	269.53	278.42	276.16	268.59
N	17	57	61	27
Radius length (mm)				
SDI	1.12	1.10	1.10	1.12
Male mean	222.42	235.94	234.46	232.66
N	11	41	41	52
Female mean	199.23	214.09	212.42	208.07
N	12	58	57	27
Femur length (mm)				
SDI	1.07	1.08	1.06	1.10
Male mean	400.36	418.00	406.55	414.37
N	17	38	49	50
Female mean	374.37	387.86	383.63	375.59
N	14	55	68	27
Tibia length (mm)				
SDI	1.08	1.09	1.06	1.09
Male mean	334.33	358.03	349.54	354.86
N	17	39	48	50
Female mean	310.68	329.71	328.48	324.86
N	13	55	68	27
Rib 1 area (mm ²)				
SDI	1.69	1.14	1.02	1.08
Male mean	1,364.11	1,933.07	1,824.68	1,073.81
N	9	31	34	18
Female mean	808.05	1,692.28	1,776.00	990.58
N	9	48	43	13

Rib 2 area (mm ²)				
SDI	1.57	1.21	1.07	1.06
Male mean	5,451.00	6,390.01	5,793.31	5,152.41
N	8	21	25	18
Female mean	3,479.84	5277.00	5,401.48	4,873.85
N	4	31	28	7
Rib 3 area (mm ²)				
SDI	1.67	1.21	1.01	1.13
Male mean	9,319.41	10,058.62	8,513.13	8,864.40
N	6	21	14	18
Female mean	5,594.68	8,341.86	8,408.42	7,787.81
N	2	32	21	11
Rib 4 area (mm ²)				
SDI	1.75	1.19	1.05	1.13
Male mean	11,715.47	12,316.53	11,062.81	10,442.36
N	4	21	13	18
Female mean	6,691.68	10,388.19	10,511.37	9,215.26
N	5	34	23	12
Rib 5 area (mm ²)				
SDI	1.50	1.15	1.12	1.08
Male mean	11,675.50	13,177.08	12,860.72	10,834.22
N	6	25	15	17
Female mean	7,744.60	11,447.58	11,440.87	10,022.20
N	2	35	23	10
Rib 6 area (mm ²)				
SDI	1.39	1.12	1.14	1.07
Male mean	11,396.31	13,444.32	13,428.85	11,085.03
N	8	22	13	16
Female mean	8,188.63	11,960.77	11,816.30	10,381.77
N	3	36	22	11
Rib 7 area (mm ²)				
SDI	1.21	1.12	1.20	1.10
Male mean	10,479.69	12,820.30	13,373.70	10,981.90
N	7	30	14	16
Female mean	8,669.77	11,468.46	11,134.58	10,019.79
N	3	41	23	11
Rib 8 area (mm ²)				
SDI	1.39	1.13	1.14	1.07
Male mean	10,269.93	12,060.59	11,856.31	10,243.81
N	7	27	21	17
Female mean	7,383.26	10,667.16	10,437.36	9,569.56
N	2	42	23	11

Rib 9 area (mm ²)				
SDI	1.40	1.13	1.08	0.97
Male mean	9,425.17	11,008.11	10,279.25	9,563.99
N	6	27	18	18
Female mean	6,731.59	9,717.00	9,480.13	9,817.13
N	4	43	27	9

Table 3: Significant differences of Bonferroni comparisons of SDI between groups. Significant differences are based on $P < 0.01$. MPC = Machu Picchu/Cuzco, SP = San Pedro de Atacama, AZ = Arica, AC = Ancón

Variable	Significant differences between groups
Body mass	AZ < MPC, SP, AC
Humerus	None
Radius	None
Femur	None
Tibia	None
Rib 1 area	MPC > SP > AC > AZ
Rib 2 area	MPC > SP > AZ & AC
Rib 3 area	MPC > SP > AC > AZ
Rib 4 area	MPC > SP & AC > AZ
Rib 5 area	MPC > SP & AC > AZ
Rib 6 area	MPC > SP & AC > AZ
Rib 7 area	MPC & AZ > SP & AC
Rib 8 area	MPC > SP & AC > AZ
Rib 9 area	MPC > SP > AC > AZ

Table 4: Sex-specific intrinsic variation values with ratios of differences between males and females by site. Ratios that indicate significantly different intrinsic variation between males and females based on comparisons with F distribution table are noted in bold face ($P < 0.01$)

	Machu Picchu/ Cuzco		San Pedro de Atacama		Arica		Ancón	
	M	F	M	F	M	F	M	F
Body mass	0.0100	0.0059	0.0065	0.0067	0.0071	0.0081	0.0081	0.0081
Ratio	1.69		1.02		1.14		1.00	
Humerus	0.0025	0.0020	0.0024	0.0021	0.0018	0.0022	0.0021	0.0016
Ratio	1.26		1.14		1.22		1.31	
Radius	0.0058	0.0041	0.0027	0.0024	0.0027	0.0024	0.0026	0.0020
Ratio	1.41		1.13		1.13		1.30	
Femur	0.0027	0.0022	0.0024	0.0019	0.0018	0.0018	0.0016	0.0014
Ratio	1.23		1.26		1.00		1.13	
Tibia	0.0045	0.0041	0.0027	0.0027	0.0025	0.0023	0.0018	0.0018
Ratio	1.09		1.00		1.09		1.00	
R1 area	0.1927	0.1764	0.0595	0.0265	0.0402	0.0448	0.0468	0.0580
Ratio	1.09		2.24		1.11		1.24	
R2 area	0.0567	0.0913	0.0318	0.0199	0.0441	0.0230	0.0177	0.0456
Ratio	1.61		1.60		1.92		2.57	
R3 area	0.0266	0.1168	0.0098	0.0136	0.0239	0.0196	0.0166	0.0239
Ratio	4.39		1.39		1.22		1.44	
R4 area	0.0105	0.0046	0.0061	0.0093	0.0257	0.0103	0.0152	0.0097
Ratio	2.28		1.52		2.49		1.57	
R5 area	0.0403	0.0596	0.0081	0.0118	0.0219	0.0066	0.0547	0.0055
Ratio	1.48		1.46		3.32		9.95	
R6 area	0.0312	0.0030	0.0097	0.0090	0.0135	0.0068	0.0107	0.0103
Ratio	10.4		1.08		1.99		1.04	
R7 area	0.0312	0.0243	0.0107	0.0135	0.0162	0.0096	0.0091	0.0144
Ratio	1.28		1.26		1.69		1.58	
R8 area	0.0343	0.0003	0.0109	0.0136	0.0121	0.0050	0.0073	0.0137
Ratio	114.33		1.25		2.42		1.88	

R9 area	0.0310	0.0005	0.0142	0.0155	0.0208	0.0087	0.0111	0.0198
Ratio	62.00		1.09		2.39		1.78	

Table 5: Intrinsic morphological variation: Significant differences between groups based on Bonferroni comparisons. MPC = Machu Picchu/Cuzco, SP = San Pedro de Atacama, AZ = Arica, AC = Ancón

Variable	Significant differences between groups at $P < 0.01$
Body mass	MPC > SP, AZ, AC; AZ > SP, AZ
Humerus	AC > MPC, SP, AZ MPC > SP
Radius	MPC > SP, AZ, AC; AC > SP, AZ
Femur	MPC & SP > AZ, AC; AC > AZ
Tibia	MPC & AZ > SP & AC
Rib 1 area	SP > AC, AZ, MPC; AC > AZ
Rib 2 area	AC > MPC, SP, AZ; AZ > MPC, SP
Rib 3 area	MPC > SP, AZ, AC; MPC > SP, AC
Rib 4 area	AZ > MPC, SP, AC; MPC > SP, AC
Rib 5 area	AC > MPC, SP, AZ; AZ > MPC, SP
Rib 6 area	MPC > SP, AZ, AC AZ > SP, AC
Rib 7 area	AZ > MPC, SP, AC AC > MPC, SP
Rib 8 area	MPC > SP, AZ, AC AZ > SP, AC AC > SP
Rib 9 area	AC > SP, AZ AZ > SP

Table 6: Levene's nonparametric test results of ANOVA for equality of variance between sexes by site. Significant differences are noted in bold.

Variable	Machu Picchu/Cuzco		San Pedro de Atacama		Arica		Ancón	
	<i>F</i> value	<i>P</i>	<i>F</i> value	<i>P</i>	<i>F</i> value	<i>P</i>	<i>F</i> value	<i>P</i>
Body mass	----	----	5.52	0.02	8.23	0.001	14.26	< 0.001
Humerus	0.76	0.39	6.94	0.01	6.40	0.01	15.17	< 0.001
Radius	0.29	0.60	7.56	0.01	6.82	0.01	15.02	< 0.001
Femur	0.75	0.39	7.82	0.01	7.34	0.01	14.29	< 0.001
Tibia	1.35	0.25	7.94	0.01	5.99	0.02	14.26	< 0.001
Rib 1 area	0.00	1.00	9.77	< 0.01	3.52	0.06	2.12	0.16
Rib 2 area	3.23	0.10	5.65	0.02	0.50	0.48	7.06	0.01
Rib 3 area	2.25	0.18	5.65	0.02	3.35	0.08	3.91	0.06
Rib 4 area	0.16	0.70	7.25	0.01	5.91	0.02	2.93	0.10
Rib 5 area	2.25	0.18	3.67	0.06	4.04	0.05	3.85	0.06
Rib 6 area	3.27	0.10	7.01	0.01	5.21	0.03	2.35	0.14
Rib 7 area	2.28	0.17	3.86	0.05	4.92	0.03	2.35	0.14
Rib 8 area	2.16	0.19	7.13	0.01	0.26	0.61	3.01	0.10
Rib 9 area	0.96	0.36	7.98	0.01	4.39	0.04	5.74	0.02