Quaternary International xxx (2017) 1–11

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Morphological signatures of high-altitude adaptations in the Andean archaeological record: Distinguishing developmental plasticity and natural selection

Karen J. Weinstein

Department of Anthropology and Archaeology, Dickinson College, Carlisle, PA, United States

ARTICLE INFO

Article history:
Received 9 August 2016
Received in revised form
2 May 2017
Accepted 2 June 2017
Available online xxx

Keywords:
Andes
High-altitude hypoxia
Body size
Rib morphology
Developmental plasticity
Natural selection

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.

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 5000 m, 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

---

E-mail address: weinstek@dickinson.edu.

http://dx.doi.org/10.1016/j.quaint.2017.06.004
1040-6182/© 2017 Elsevier Ltd and INQUA. All rights reserved.

Please cite this article in press as: Weinstein, K.J., Morphological signatures of high-altitude adaptations in the Andean archaeological record: Distinguishing developmental plasticity and natural selection, Quaternary International (2017), http://dx.doi.org/10.1016/j.quaint.2017.06.004

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.

Please cite this article in press as: Weinstein, K.J., Morphological signatures of high-altitude adaptations in the Andean archaeological record: Distinguishing developmental plasticity and natural selection, Quaternary International (2017), http://dx.doi.org/10.1016/j.quaint.2017.06.004