

Introduction

Contributions of A. Roberto Frisancho to Human Population Biology: An Introduction

WILLIAM R. LEONARD*

Department of Anthropology, Northwestern University, Evanston, Illinois 60208

This article was presented at the 2008 AAPA meeting in a symposium in honor of A. Roberto Frisancho, on the occasion of his retirement from the Department of Anthropology of the University of Michigan

ABSTRACT Over the span of his career, A. Roberto Frisancho has been one of the prime architects of the development and expansion of human population biology. His research and scholarly publications have helped to move the field beyond simple descriptions of human variation to address the nature and evolutionary origins of human biological diversity. Frisancho's early work in the Peruvian Andes elegantly demonstrated the importance of developmental acclimatization for promoting adaptive responses to the multiple stressors of high-altitude environments. Since mid-1970s, he has played a major role in developing and expanding the use of anthropometric techniques for assessing physical growth and nutritional status. Frisancho's influential publications have helped to make the use of anthropometric methods commonplace in the fields of nutritional science and public health. Throughout his career, Frisancho's work has examined how environmental, genetic, and developmental factors interact to influence human health and nutritional status. His research has addressed topics ranging from the determinants of low-birth weight infants in teenage mothers to the origins of obesity and associated metabolic diseases in populations of the developing world. Both the breadth and impact of Frisancho's work have been truly remarkable. The field of human population biology owes much to the tremendous contributions of A. Roberto Frisancho. Am. J. Hum. Biol. 21:599–605, 2009. © 2009 Wiley-Liss, Inc.

Since the original pioneering research done during the 1960s as part of the Human Adaptability Project of the International Biological Programme, the field of human population biology has expanded and matured, moving beyond simple descriptions of human variation to explicitly address the nature and evolutionary origins of human biological diversity (Baker and Little, 1976; Baker and Wiener, 1966; Milan, 1980; Stinson et al., 2000). Over this time A. Roberto Frisancho of the University of Michigan has been one of the principal architects of the development of human biology and adaptability. Frisancho's ground-breaking research, influential writing, and skilled graduate mentoring have had a profound impact on current research directions in human biology.

The papers in this issue—by students and postdoctoral fellows of Frisancho's—explore recent advances in our understanding of human adaptive strategies and population variation in health. Each of the papers will address issues strongly shaped by Frisancho's work including: (1) functional adaptation to high altitude, (2) methodological innovations for assessing variation in growth, and (3) adaptive and evolutionary perspectives on human health and nutrition.

This introduction provides an overview of the major research domains that Roberto has addressed during of his career. Both the topics that Roberto has chosen to study and the perspective that he has brought to his work have had a lasting impact on our field. That impact is clearly reflected in the work presented in each of the papers in this issue.

HUMAN ADAPTATION: NUÑOA AND BEYOND

Among Frisancho's best known work is his research on high-altitude physiology and development. As a member of the Pennsylvania State University High Altitude Research group directed by Paul T. Baker (see Fig. 1), Roberto carried out of his Master's and doctoral research

in the Nuñoa district of the Southern Peruvian Andes between 1964 and 1966 (Frisancho, 1966, 1969). Roberto's early publications demonstrated the importance of developmental acclimatization for promoting adaptive responses to the multiple stressors of high-altitude (HA) environments. His 1970 paper on "altitude and growth" in the *American Journal of Physical Anthropology* (Frisancho and Baker, 1970) was the first to systematically document the slow and prolonged growth in stature and body mass and the accelerated growth rate of chest dimensions in the indigenous Quechua highlanders.

Through the early-1970s, Roberto continued to explore the influence of altitude on diverse aspects of human biology, including (1) lung function (Frisancho et al., 1973c), (2) aerobic capacity (Frisancho et al., 1973a, 1975b), (3) skeletal development (Frisancho et al., 1970d), and (4) neonatal and infant mortality (Frisancho et al., 1973b; Frisancho and Cossman, 1970). In 1975, he synthesized all the relevant literature on functional adaptation to HA hypoxia in a major review in *Science* (Frisancho, 1975). With remarkable clarity the paper systematically laid out the different "strategies" employed by HA natives versus sea-level "sojourners" to adjust to low oxygen availability. Figure 2 shows the summary flow diagram from the paper highlighting the contributions of the different functional systems to adapting to hypoxic stress—pulmonary ventilation, pulmonary diffusion, and vascular/hematologic.

The paper also presented the core of what Roberto later expanded into the "Developmental Adaptation Model"

*Correspondence to: William R. Leonard, Department of Anthropology, Northwestern University, 1810 Hinman Avenue, Evanston, IL 60208, USA. E-mail: w-leonard1@northwestern.edu

Received 18 January 2009; Accepted 4 February 2009

DOI 10.1002/ajhb.20916

Published online 14 April 2009 in Wiley InterScience (www.interscience.wiley.com).

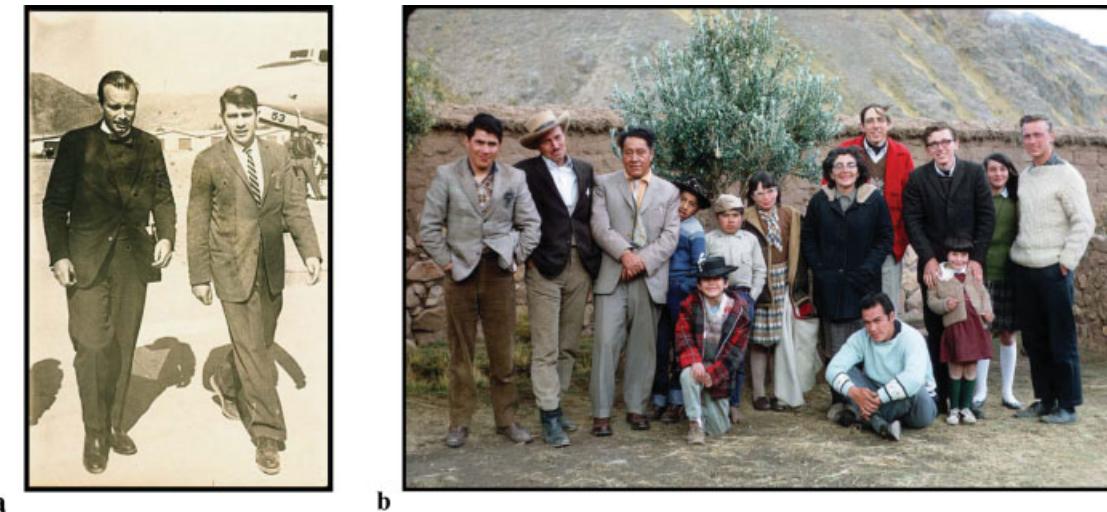


Fig. 1. The early days of high altitude research in Peru. (a) Roberto Frisancho meets Paul Baker at the Cusco airport during Baker's first visit to Peru in 1962 (photo courtesy of Thelma Baker). (b) The Penn State High Altitude Research Team, Hutan Cruz Hacienda, Nuñoa District, Peru, 1964. From left are: Roberto Frisancho, Paul Baker, Lucas Guerra, Jefferson Guerra, Joshua Baker, unidentified child, Amy Baker, Thelma Baker, Victor Barreda, Brooke Thomas, Mike Little, Felicia Baker, Deborah Baker, and Tony Way (photo courtesy of Tony Way). [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

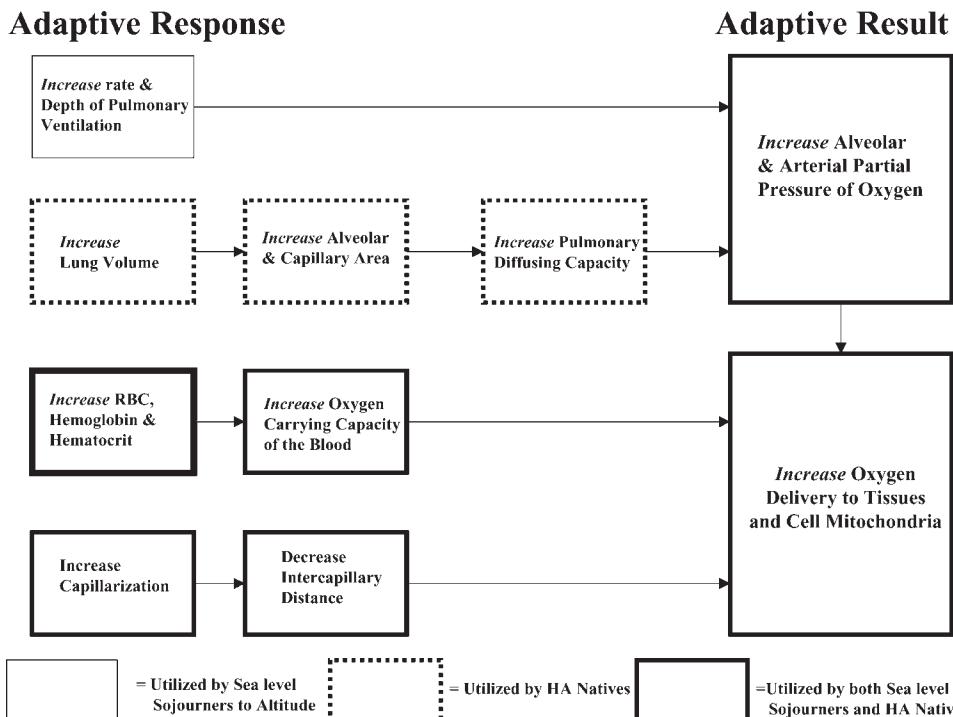
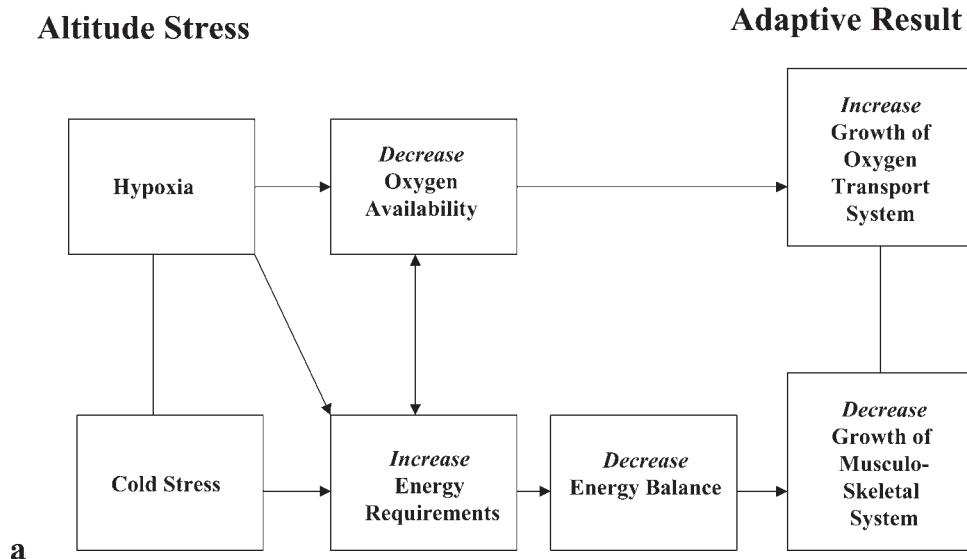


Fig. 2. Flow diagram outlining the alternative adaptive pathways utilized by sea level sojourners and high altitude (HA) natives in response to HA hypoxia. Adaptation to HA hypoxia involves the integration of different functional systems: (a) pulmonary ventilation, (b) pulmonary diffusion, and (c) vascular/hematologic. Both HA natives and sojourners increase red blood cell production and increase capillarization in the peripheral tissue to enhance the effectiveness of oxygen transport and delivery in the blood. Developmental increases in lung volume and alveolar surface area result in enhanced pulmonary diffusing capacity in lungs of HA natives. In contrast, sojourners have smaller lung volumes, and thus respond by increasing the rate and depth of their breathing (increased pulmonary ventilation) (modified from Frisancho, 1975).

(DAM). This model (Fig. 3, adapted from Frisancho (1993) shows how exposure to the key stressors of high altitude during growth is responsible for explaining the origin of the distinctive physical characteristics of native high-

landers—(1) slow growth and resultant small adult body size, (2) delayed physical and sexual maturation, (3) expanded chest dimensions and lung volume, and (4) the signature of “complete” functional adaptation to HA hy-



Full Acclimatization to HA Hypoxia

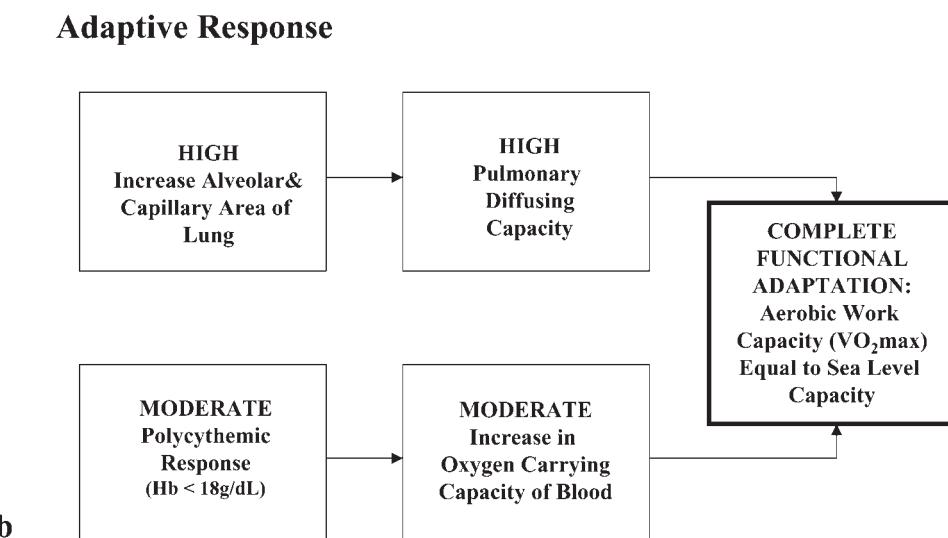


Fig. 3. Flow diagrams presenting the central pathways utilized by native populations to adapt to the multiple stressors of HA environments. (a) At high altitude, the joint effects of hypoxic and cold stress promote increased energy demands, resulting in slowed musculo-skeletal growth and small adult body size. In contrast, hypoxic stress accelerates the growth of organs of the oxygen transport system, resulting in the enlarged lungs and hearts. (b) Physiological pathways used by HA natives to achieve “complete functional adaptation” to HA hypoxia. HA natives show increased alveolar and capillary areas in their lungs (relative to sea level sojourners), contributing to high pulmonary diffusing capacity. Additionally, they show modest increases in hemoglobin levels over sea level values, resulting in increased oxygen carrying capacity of the blood-stream. Complete function adaptation is measured as maximal working capacities ($VO_2\text{max}$) at altitude being comparable to sea level values (modified from Frisancho, 1993).

poxia—achievement of maximal aerobic capacities that are comparable to sea-level norms (Frisancho, 1975, 1976, 1981a, 1993).

The DAM continues to shape the ways that we think about and research HA biology today. Although subsequent research has identified important genetic differ-

ences in the adaptive pathways used by different HA populations (see Beall, 2000, 2007; Beall et al., 2004; Moore et al., 1998, 2006) the model continues to provide an important explanatory framework for understanding variation in HA physiology (Beall, 2007; Julian et al., 2009). Moreover, Frisancho’s DAM presages many of the ele-

ments of the research domain now known as: "Developmental Origins of Health and Diseases" (the DoHaD concept; see Barker, 1998; Kuzawa, 2007; Prentice, 2005). With the rise of the Developmental Origins concept in biomedical research, perspectives from human adaptability and evolutionary biology are now helping to inform our understanding of the causes and potential treatments for a variety of chronic health problems.

By the mid-1970s, the focus of Roberto's work expanded beyond HA to broader considerations of human adaptation to environmental stressors. His field project in province of Lamas, Peru, from 1973 to 1977 examined the influence of genetics, environment, nutrition, and socioeconomic status on the growth of lowland Quechua children, compared to their highland counterparts (Frisancho et al., 1975a, 1980; Stinson and Frisancho, 1978). This research showed that, contrary to expectations, the lowland children appeared to be experiencing greater nutritional stress, as they were shorter and lighter, and had lower skinfold and arm muscle measures than their HA peers (Frisancho et al., 1975a). Yet despite their shorter stature, lowland children had relatively longer arms and legs, contributing to a more linear body build. Thus, the differences in body proportions between the two groups appear to have been shaped more by differences in temperature and altitude than socioeconomic or nutritional factors (Stinson and Frisancho, 1978).

At the end of the 1970s, Roberto began to synthesize the available literature on human adaptation to all the major environmental stressors (i.e., temperature, solar radiation, altitude, and nutrition). In 1979, he published the first edition of his textbook on the subject—*Human Adaptation: A functional interpretation* (CV Mosby; Frisancho, 1979). The book was republished by the University of Michigan Press (Frisancho, 1981a), and expanded into the current edition—*Human Adaptation and Accommodation* in 1993 (Frisancho, 1993). The current edition of the book remains the essential text for courses in human adaptability.

In his most recent textbook, *Humankind Evolving* (Frisancho, 2006), Roberto applies the principles of human adaptation to understand the origin and nature of contemporary human diversity. The book provides a fresh and innovative perspective on biological anthropology that is departure from the standard approaches used in introductory texts. As such, it is a valuable reference for both undergraduate and graduate students in biological anthropology.

"THE GROWTH OF GROWTH": ANTHROPOMETRIC STANDARDS AND NUTRITIONAL ASSESSMENT

When he arrived at the University of Michigan in 1969, Roberto joined forces with Stanley Garn and established Michigan as a center for research and training in human growth and development. During the 1970s, Frisancho and Garn collaborated on number of projects including the Ten State Nutrition Survey and a study with the Instituto de Nutrición de Centro América y Panamá on the nutritional health and skeletal development in Central American populations (Frisancho et al., 1970a,b,c, 1971a,b; Frisancho and Garn, 1971a,b; Garn et al., 1971, 1972). It was, in part, these diverse experiences with using anthropometric methods that provided Roberto with the opportunity to begin developing norms for assessing growth patterns in children and nutritional well-being in adults.

With his 1974 publication on norms for fatness and arm muscularity in the *American Journal of Clinical Nutrition* (Frisancho, 1974), Roberto began to establish himself at "the Standards Man." Since that time, Roberto's influential publications have helped to make the use of anthropometric norms commonplace in the fields of nutritional science and public health. Indeed, Roberto's three most widely cited refereed publications (each cited more than 200 times) are papers on anthropometric standards that were published in the *American Journal of Clinical Nutrition* (Frisancho, 1974, 1981b, 1984). These norms have been widely reprinted in introductory and advanced texts in human nutrition (e.g., Duggan, 2008; Edelstein, 2007; Gibson, 2005; Samour, 2005), and his own books—*Anthropometric Standards for the Assessment of Growth and Nutritional Status* (Frisancho, 1990), and the recently published *Anthropometric Standards: An Interactive Nutritional Reference of Body Size and Body Composition for Children and Adults* (Frisancho, 2008) are standard reference texts in both human biology and human nutritional science.

EVOLUTIONARY AND ADAPTIVE PERSPECTIVES ON HUMAN NUTRITION AND HEALTH

Throughout his career, Roberto has also been at the forefront of applying the evolutionary and adaptive perspectives from human biology to tackle major public health issues. In the 1970s and early-1980s, Roberto collaborated with colleagues at the Maternity Hospital in Lima to study the nutritional and developmental determinants of low-birth weight infants (Frisancho et al., 1977, 1983, 1984b,c, 1985). This work highlighted the important role that maternal nutritional status has on the trajectory of a child's prenatal and postnatal growth. Contrary to the prevailing notions of the time, Roberto's work showed that the fetal growth was not buffered from fluctuations in maternal nutritional status; but rather, that maternal undernutrition had a profound influence on childhood development and later health outcomes (Frisancho et al., 1977).

Additionally, this research demonstrated that fetal-maternal competition for nutrients played a major role in the origin of low-birth weight infants among teenage mothers. Because teen mothers are still growing, they require greater nutritional increases during pregnancy to produce a normal birth weight baby (Frisancho et al., 1985). These findings helped to reshape nutritional recommendations for adolescent mothers during the 1980s (Kramer, 1987; Stevens-Simon and McAnarney, 1988).

The biocultural origins of hypertension among African-Americans is another issue that Roberto has explored in depth over the last 25 years. Beginning in the mid-1980s, Roberto used the NHANES data sets to investigate the genetic and nutritional determinants of elevated blood pressure in African-Americans (Frisancho et al., 1984a). This work suggested that greater sodium sensitivity combined with low-potassium intakes contributed to the increased risks of hypertension in the African-American community.

By the mid-1990s, a growing debate had emerged over the relative contributions of genes, lifestyle, and the legacy of slavery to elevated blood pressure among populations of the African diaspora (see Blaustein and Grim, 1991; Curtin, 1992; Dressler, 1991; Rotimi and Cooper,

1997; Wilson and Grim, 1991). In this context, Roberto initiated a study of blood pressure among a population of African descent living in the middle altitude Yungas region of Bolivia. The choice of this study group was particularly novel, because Afro-Bolivians of the Yungas are, on average, wealthier and better educated than the Aymara and Mestizo populations with whom they share their communities. Thus, Roberto and his colleagues were able to explore blood pressure variation in an African diaspora population that was not living an economically marginalized situation. This work demonstrated that Afro-Bolivians, despite their relatively better economic standing, had significantly higher BP levels than their Aymara counterparts living in the same community (Frisancho et al., 1999). Thus, while it is clear that socio-economic and lifestyle factors play a major role in the development of hypertension in populations of the African diaspora, it appears likely that a genetic-environmental dynamic may be at play.

Most recently, Roberto's research has examined the origins of the growing rates of obesity among urbanizing regions of the developing world (Frisancho, 2003, 2007). Unlike in the industrialized world, obesity is a relatively recent phenomenon in developing nations and is one that is often co-exists with high rates of undernutrition. Drawing on both primary analyses and on published research, Frisancho has argued that early life undernutrition and adult obesity are, in many respects, two sides of the same coin. He has shown that reduced relative leg length—an indicator of poor childhood growth—is associated with increased body fatness and risks of obesity among populations in the US and Latin America (Frisancho, 2007). Drawing on recent metabolic studies in Brazil (e.g., Hoffman et al., 2000), he further suggests that chronic undernutrition and growth stunting during childhood predisposes individuals to adult obesity by reducing their ability to burn fat (Frisancho, 2003). This work highlights the developmental origins of "thrifty metabolism" and their implications for the emergence of obesity and cardiovascular disease.

Overall, what has been most impressive about Roberto's work on applying evolutionary approaches to the study of human health and disease is his ability to effectively present these complex issues to a broad audience. Roberto has been one of Michigan's most popular undergraduate teachers, having received the University's "Excellence in Education" four times (1994, 1996, 1997, and 1998), and in 1997, he received the "Amoco Distinguished faculty Achievement Award." In 2000, he was awarded the prestigious Arthur Thurnau Professorship for distinguished teaching, and in 2006 in recognition for his outstanding work in Andean Human biology Roberto was bestowed with the title of Honorary Professor of the National University of San Antonio Abad of Cusco, Perú.

THE PAPERS

Those of us who have worked closely with Roberto have benefited immensely from his broad research experience and his generous spirit. Each of the papers in this issue build upon foundations that he established.

Papers by Sara Stinson and Colleen Julian and colleagues address advancements in our understanding of HA biology and adaptation. Stinson specifically examines the multiple factors—genetics, hypoxic stress, and nutri-

tional stress—that contribute to the development of relative sitting height in two groups of HA children from Bolivia: (1) indigenous Aymara children from poor, rural circumstances, and (2) and upper-income children from the city of La Paz. The variation in body proportions within and between the two groups is suggestive of a mix of genetic, nutritional, and ecological factors.

Colleen Julian, Megan Wilson, and Lorna Moore explore the physiological mechanisms used by native HA women to promote fetal growth and normal birth weights in the face of hypoxic stress. The authors note that in studying adaptation to HA stressors, a focus on pregnancy outcomes is particularly relevant, because they are direct determinants of reproductive success. Recent advancements in statistical genetic techniques are now allowing us to understand the genetic basis of key functional adaptations for preserving fetal growth among native HA populations.

Shelley Smith and Peter Buschang tackle fundamental questions of normative growth, examining the development of canine and premolar roots in a longitudinal sample of American children. These data are important both for (1) understanding normal patterns of dental development in modern human populations, and (2) establishing comparative standards for evaluating life history patterns in early hominids.

Papers by David Tracer, Elizabeth Abrams and Steven Meshnick, Susan Tanner and colleagues, Inès Varela-Silva and colleagues, William Leonard and colleagues, Robin Nelson, and Lillian Gleiberman each consider developmental and/or ecological influences on human health and nutrition status.

David Tracer draws on his rich data on breastfeeding patterns among the Au and Gnau of Papua New Guinea to test key predictions of parental investment theory. Tracer notes that lactation is a very costly form of parental investment, particularly among groups like the Au where mothers nurse their children for almost 4 years. Contrary to expectations, mothers showed greater rather than less investment in infants of poor nutritional status. This study demonstrates the utility of linking behavioral information on infant feeding patterns with standard measures of children's nutritional status to test important questions about human evolutionary biology.

Like Tracer, Elizabeth Abrams and Steven Meshnick draw on evolutionary theory to examine an important global health problem—the impact of malarial infections on women and infants. Specifically, Abrams and Meshnick use malarial infections (and infectious diseases more broadly) during pregnancy as a novel window onto parent-offspring conflicts and trade offs. The authors summarize what is known about the proximate mechanisms through which malaria causes more severe or frequent infections for pregnant and nonpregnant women. By drawing on evolutionary models of parent-offspring conflict (Trivers, 1974), they are able to make explicit predictions about how the timing of malarial infections during pregnancy will result in different health outcomes for the mother and infant.

Susan Tanner and colleagues examine the influence of parasitic infections on measures of growth and nutritional status of indigenous Tsimane' children from lowland Bolivia. It has long been recognized that infectious diseases interact with malnutrition to contribute to poor childhood growth in rural parts of the developing world; however, in-

fectious and parasitic disease loads are not commonly measured in most anthropological studies of child growth. Tanner and colleagues document high levels of both intestinal parasitism and linear growth stunting among Tsimane' children 2–10 years of age. These findings indicate that parasitic infections play a strong role in shaping the health of children in this rural, tropical environment.

Inês Varela-Silva and colleagues investigate maternal influences on child growth and obesity risks among Maya children from Merida, Mexico. Their analyses show that both maternal stature and child's birth weight are significant predictors of whether that child will be overweight at ages 4–6 years. Smaller maternal stature and lower birth weights are associated with reduced risks of a child being overweight. This work underscores the importance of intergenerational influences on human growth and nutritional health.

Leonard and colleagues examine the influence of linear growth retardation on fat oxidation and obesity risks among indigenous Siberians (the Buryat) undergoing changes in diet and activity patterns. They find that shorter Buryat women have significantly lower levels of fat oxidation, higher body fat, and higher serum lipid levels than their taller counterparts. These findings are similar to previous work, suggesting that reduced fat metabolism is a mechanism through which early life growth stunting may increase obesity risks in adulthood.

Similarly, Robin Nelson's paper also addresses how differences in nutritional environment during development may shape later life obesity risks. Drawing a sample of adult men and women from Jamaica, she finds that individuals who grew up during the economically-turbulent period after the country's independence from Britain (in 1962) have significantly higher age-adjusted BMIs and skinfold measures than those of other age cohorts. Thus, Nelson's findings suggest that conditions of nutritional deprivation in the 1960s and 1970s in Jamaica may have predisposed that birth cohort to increased obesity risks in adulthood.

Lillian Gleiberman's paper addresses the long-standing question of how variation in sodium consumption and excretion influences risks for hypertension. While there is substantial evidence that limiting salt intake can help reduce blood pressure in at least some individuals, the question of whether genetic differences in sodium/salt sensitivity underlie major ethnic variation in hypertension risks remains a hotly debated topic. Gleiberman provides a broad review of the major research studies on salt sensitivity and blood pressure over the last quarter century. This work highlights the need for further integration of research on genetic, sociodemographic, and nutritional influences on blood pressure to provide a more complete picture of the origin and nature of population-differences in hypertension.

Rachel Albalak gives us an overview of her extensive applied research experiences with the CDC on epidemiological approaches to the study of infectious diseases. She specifically describes her work with two large, multisite programs: (1) the Tuberculosis Epidemiologic Studies Consortium and (2) the Emerging Infections Programs. Her paper highlights the shared perspectives of biological anthropology and applied public health.

Roberto Frisancho concludes this issue by providing his thoughts on future directions for research on human adaptation and population variation in health. Throughout his career, Frisancho's work has demonstrated the

utility of the developmental adaptation framework for understanding the nature of human biological variability. His article summarizes two important examples of developmental adaptation: (1) the attainment of enlarged residual lung volume among indigenous Andean populations in response to HA hypoxia and (2) the emergence of a "thrifty phenotype" (i.e., increased energetic efficiency and obesity risks) among individuals who have grown up under poor nutritional circumstances. He further notes how ongoing research in epigenetics is blurring the lines between our traditional notions of "functional" versus "genetic" adaptations. Indeed, we are now coming to realize the important role that environmental factors (e.g., diet, activity, and environmental pollutants) have in turning "on" or "off" the expression of key genes that regulate metabolism and health.

As he has done for the last 40 years, Roberto reminds us of the critical role that the field of human biology has to play in understanding the human condition. We sincerely thank him for leading the way!

ACKNOWLEDGMENT

The articles in this issue were initially presented in the Symposium, "Integrative Approaches to the Study of Human Adaptation and Population Health: A Symposium in Honor of A. Roberto Frisancho", on April 11, 2008 at the Annual Meetings of the American Association of Physical Anthropologists (AAPA) and Human Biology Association (HBA) in Columbus, Ohio. The symposium participants and I are most grateful to Roberto for his mentoring, guidance, and friendship over the years. He has been a tremendous part of all of our lives.

LITERATURE CITED

- Baker PT, Little MA (editors). 1976. *Man in the Andes: a multi-disciplinary study of high-altitude Quechua*. Dowden, Stroudsburg, PA: Hutchinson and Ross.
- Baker PT, Wiener JS (editors). 1966. *The biology of human adaptability*. Oxford: Clarendon Press.
- Barker DJP. 1998. In utero programming of chronic disease. *Clin Sci* 95:115–128.
- Beall CM. 2000. Tibetan and Andean patterns of adaptation to high-altitude hypoxia. *Hum Biol* 72:201–228.
- Beall CM. 2007. Two routes to functional adaptation: Tibetan and Andean high-altitude natives. *Proc Natl Acad Sci USA* 104:8655–8660.
- Beall CM, Song K, Elston RC, Goldstein MC. 2004. Higher offspring survival among Tibetan women with high oxygen saturation genotypes residing at 4,000 m. *Proc Natl Acad Sci USA* 101:14300–14304.
- Blaustein MP, Grim CE. 1991. The pathogenesis of hypertension: black-white differences. *Cardiovasc Clin* 21:97–114.
- Curtin PD. 1992. The slavery hypothesis for hypertension among African Americans: the historical evidence. *Am J Public Health* 82:1681–1686.
- Dressler WW. 1991. Social class, skin color, and arterial blood pressure in two societies. *Ethnic Dis* 1:60–77.
- Duggan A. 2008. Nutrition in pediatrics: basic science, Clinical Applications, 4th ed. Hamilton, ON: BC Decker.
- Edelstein S. 2007. *Rapid reference for nurses: nutrition*. Sudbury, MA: Jones and Bartlett.
- Frisancho AR. 1966. Human growth in a high altitude peruvian population. Masters Thesis, Pennsylvania State University, University Park, PA.
- Frisancho AR. 1969. Human growth, physique, and pulmonary function at high altitude: a field study of a Peruvian Quechua population, Ph.D. thesis, Pennsylvania State University, University Park, PA.
- Frisancho AR. 1974. Triceps skin folds and upper arm muscle size norms for assessment of nutritional status. *Am J Clin Nutr* 27:1052–1058.
- Frisancho AR. 1975. Functional adaptation to high altitude hypoxia. *Science* 187:313–319.
- Frisancho AR. 1976. Growth and morphology at high altitude. In: Baker PT, Little MA, editors. *Man in the Andes: a multi-disciplinary study of high-altitude Quechua*. Stroudsburg, PA: Hutchinson and Ross. p 180–207.

- Frisancho AR. 1979. Human Adaptation: a functional interpretation. St. Louis: CV Mosby.
- Frisancho AR. 1981a. Human adaptation: a functional interpretation, 2nd ed. Ann Arbor, MI: University of Michigan Press.
- Frisancho AR. 1981b. New norms of upper limb fat and muscle areas for assessment of nutritional status. *Am J Clin Nutr* 34:2540–2545.
- Frisancho AR. 1984. New standards of weight and body composition by frame size and height for assessment of nutritional status of adults and the elderly. *Am J Clin Nutr* 40:808–819.
- Frisancho AR. 1990. Anthropometric standards for the assessment of growth and nutritional status. Ann Arbor, MI: University of Michigan Press.
- Frisancho AR. 1993. Human adaptation and accommodation. Ann Arbor, MI: University of Michigan Press.
- Frisancho AR. 2003. Reduced rate of fat oxidation: a metabolic pathway to obesity in the developing nations. *Am J Hum Biol* 15:522–532.
- Frisancho AR. 2006. Humankind evolving. Exploration on the origins of human diversity. Dubuque, IA: Kendall/Hunt Publishing Co.
- Frisancho AR. 2007. Relative leg length as a biological marker to trace the developmental history of individuals and populations: growth delay and increased body fat. *Am J Hum Biol* 19:500–508.
- Frisancho AR. 2008. Anthropometric standards: an interactive nutritional reference of body size and body composition for children and adults. Ann Arbor, MI: University of Michigan Press.
- Frisancho AR, Baker PT. 1970. Altitude and growth: a study of the patterns of physical growth of a high altitude Peruvian Quechua population. *Am J Phys Anthropol* 32:279–292.
- Frisancho AR, Borkan GA, Klayman JE. 1975a. Pattern of growth of lowland and highland Peruvian Quechua of similar genetic composition. *Hum Biol* 47:233–243.
- Frisancho AR, Cossman J. 1970. Secular trend in neonatal mortality in the mountain states. *Am J Phys Anthropol* 32:103–105.
- Frisancho AR, Farrow S, Friedenzo J, Johnson T, Kapp B, Miranda C, Perez M, Rauchle I, Sanchez N, Swaninger K, Wheatcroft G, Woodill L, Ayllon I, Soria R, Rodriguez A, Machicao J. 1999. Role of genetic and environmental factors in the increased blood pressures of Bolivian Blacks. *Am J Hum Biol* 11:489–498.
- Frisancho AR, Garn SM. 1971a. Skin-fold thickness and muscle size: Implications for developmental status and nutritional evaluation of children from Honduras. *Am J Clin Nutr* 24:541–546.
- Frisancho AR, Garn SM. 1971b. The implications of skinfolds and muscle size to developmental and nutritional status of Central American children. III. Guatemala. *Trop Geogr Med* 23:167–172.
- Frisancho AR, Garn SM, Ascoli W. 1970a. Unequal influence of low dietary intakes on skeletal maturation during childhood and adolescence. *Am J Clin Nutr* 23:1220–1227.
- Frisancho AR, Garn SM, Ascoli W. 1970b. Childhood retardation resulting in reduction of adult body size due to lesser adolescent skeletal delay. *Am J Phys Anthropol* 33:325–336.
- Frisancho AR, Garn SM, Ascoli W. 1970c. Subperiosteal and endosteal bone apposition during adolescence. *Hum Biol* 42:639–664.
- Frisancho AR, Garn SM, Ascoli W. 1971a. Unaltered cortical area of pregnant and lactating women: studies of the second metacarpal bone in North and Central American populations. *Invest Radiol* 6:119–121.
- Frisancho AR, Garn SM, McCreery LD. 1971b. Relationship of skinfolds and muscle size to growth of children. I. Costa Rica. *Am J Phys Anthropol* 35:85–90.
- Frisancho AR, Guire K, Babler W, Borkan G, Way A. 1980. Nutritional influence on childhood development and genetic control of adolescent growth of Quechuas and mestizos from the Peruvian lowlands. *Am J Phys Anthropol* 52:367–375.
- Frisancho AR, Klayman JE, Matos J. 1977. Newborn body composition and its relationship to linear growth. *Am J Clin Nutr* 30:704–711.
- Frisancho AR, Leonard WR, Bollettino LA. 1984a. Blood pressure in blacks and whites and its relationship to dietary sodium and potassium intake. *J Chron Dis* 37:515–520.
- Frisancho AR, Martinez C, Velasquez T, Sanchez J, Montoye H. 1973a. Influence of developmental adaptation on aerobic capacity at high altitude. *J Appl Physiol* 34:176–180.
- Frisancho AR, Matos J, Bollettino LA. 1984b. Role of gynecological age and growth maturity status in fetal maturation and prenatal growth of infants born to young still-growing adolescent mothers. *Hum Biol* 56:583–593.
- Frisancho AR, Matos J, Bollettino LA. 1984c. Influence of growth status and placental function on birth weight of infants born to young still-growing teenagers. *Am J Clin Nutr* 40:801–807.
- Frisancho AR, Matos J, Flegel PN. 1983. Maternal nutritional status and adolescent pregnancy outcome. *Am J Clin Nutr* 38:739–746.
- Frisancho AR, Matos J, Leonard WR, Yaroch LA. 1985. Developmental and nutritional determinants of pregnancy outcome among teenagers. *Am J Phys Anthropol* 66:247–261.
- Frisancho AR, Newman MT, Baker P. 1970d. Differences in stature and cortical thickness among highland Quechua Indian boys. *Am J Clin Nutr* 23:382–385.
- Frisancho AR, Sanchez J, Pallardel D, Yanez L. 1973b. Adaptive significance of small body size under poor socio-economic conditions in southern Peru. *Am J Phys Anthropol* 39:255–262.
- Frisancho AR, Velasquez T, Sanchez J. 1973c. Influence of developmental adaptation on lung function at high altitude. *Hum Biol* 45:585–594.
- Frisancho AR, Velasquez T, Sanchez J. 1975b. Possible adaptive significance of small body size in the attainment of aerobic capacity among high-altitude Quechua natives. In: Watts ES, Johnston FE, Lasker GW, editors. *Biosocial interrelations in population adaptation*. The Hague: Mouton Publishers. p 55–64.
- Garn SM, Frisancho AR, Poznanski AK, Schweitzer J, McCann MB. 1971. Analysis of triquetral-lunate fusion. *Am J Phys Anthropol* 34:431–434.
- Garn SM, Frisancho AR, Sandusky ST, McCann MB. 1972. Confirmation of the sex difference in continuing subperiosteal apposition. *Am J Phys Anthropol* 36:377–380.
- Gibson RS. 2005. Principles of nutritional assessment, 2nd ed. Oxford: Oxford University Press.
- Hoffman DJ, Sawaya AL, Verreschi I, Tucker KL, Roberts SB. 2000. Why are nutritionally stunted children at increased risk of obesity? Studies of metabolic rate and fat oxidation in Shanty town children from São Paulo, Brazil. *Am J Clin Nutr* 72:702–707.
- Julian CG, Wilson MJ, Moore LG. 2009. Evolutionary adaptation to high altitude: a view from in utero. *Am J Hum Biol* DOI 10.1002/ajhb.20900.
- Kramer MS. 1987. Determinants of low birth weight: methodological assessment and meta-analysis. *Bull World Health Org* 65:663–737.
- Kuzawa CW. 2007. Developmental origins of life history: growth, productivity, and reproduction. *Am J Hum Biol* 19:654–661.
- Milan FA, editor. 1980. The human biology of circumpolar populations. Cambridge: Cambridge University Press.
- Milan FA, editor. 2000. The biology of circumpolar populations. Cambridge: Cambridge University Press.
- Moore LG, Niermeyer S, Zamudio S. 1998. Human adaptation to high altitude: Regional and life-cycle perspectives. *Yrbk Phys Anthropol* 41:25–64.
- Moore LG, Shriner M, Bemis L, Vargas E. 2006. An evolutionary model for identifying genetic adaptations to high altitude. *Adv Exp Med Biol* 588:101–118.
- Prentice AM. 2005. Early influences on human energy regulation: thrifty genotypes and thrifty phenotypes. *Physiol Behav* 86:640–645.
- Rotimi C, Cooper R. 1997. Hypertension in blacks. *Am J Hypertens* 7:804–812.
- Samour P. 2005. *Handbook of pediatric nutrition*, 3rd ed. Sudbury, MA: Jones and Bartlett.
- Stevens-Simon C, McAnarney ER. 1988. Adolescent maternal weight gain and low birthweight: A multifactorial model. *Am J Clin Nutr* 47:948–953.
- Stinson S, Bogin B, Huss-Ashmore R, O'Rourke D, editors. 2000. *Human biology: an evolutionary and biocultural perspective*. New York: Wiley-Liss.
- Stinson S, Frisancho AR. 1978. Body proportions of highland and lowland Peruvian Quechua children. *Hum Biol* 50:57–68.
- Trivers RL. 1974. Parent-offspring conflict. *Am Zool* 14:249–264.
- Wilson TW, Grim CE. 1991. Biohistory of slavery and blood pressure differences in blacks today: A hypothesis. *Hypertension* 17:I122–I128.