

Second Edition



HUMAN BIOLOGY

An Evolutionary and Biocultural Perspective

EDITED BY SARA STINSON
BARRY BOGIN
DENNIS O'ROURKE

 **WILEY-BLACKWELL**



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Cover: A Medieval European winter camp (drawing by Susan Carroll). The biocultural nature of human existence is depicted in this scene. Human biology is best explained by a combination of evolution and an understanding of the interaction between human biology and culture (a biocultural approach). Human ancestors originally evolved in the tropics and this means that the human species is not biologically well adapted to extreme cold. We deal with cold-behaviorally and culturally—we wear clothing, build shelters, and make fires. Even so, human populations living in cold climates have some ability to make biological adjustments to keep their hands warm in extreme cold, such as increasing blood flow to the fingers (called vasodilation). This helps with activities, such as the chopping wood and cooking, which in the times before modern gloves required that hands be exposed for fine manipulation. Cold induced vasodilation is a response that probably results from evolutionary adaptations to long term exposure to cold and from our ability to modify biology and behavior during our lifetime, our plasticity. The foods that human eat, the stages in our life cycle, and our energetic requirements are among the other aspects of human biology depicted in this scene that are best explained by an evolutionary and biocultural perspective.

PREFACE

This book is a collaborative effort by members of the Human Biology Association (www.humbio.org) to provide an introduction to the field of human biology. Human biology deals with understanding the extent of human biological variability, with explaining the mechanisms that create and pattern this variability, and with relating it to health, disease, and the social issues that concern all individuals today. Human biology relies heavily on an evolutionary perspective to explain variation through space and time, but also considers the effect that human culture has had on our biology, a biocultural perspective, to be crucial.

This book covers the major areas of human biology: genetic variation, variation related to climate, infectious and noninfectious diseases, stress, growth, aging, and demography. Each chapter is written by an authority in the field in order to provide expert coverage of these topics. Boxed text within the chapters explains the methods that human biologists use. Important terms are defined in the glossary, with each glossary term appearing in bold type the first time it is used in a chapter. Each chapter of this book begins with a list of “big questions” related to the topic of the chapter. It is the hope of all the chapter authors that when readers finish this text, they will be able to add their own lists of “big questions.” Indeed, perhaps readers will be able to make such lists well before completing all chapters. A set of recommended readings at the end of each chapter directs students to sources that will provide a good introduction to the topics covered in the book.

We thank the members of the Human Biology Association for their continuing enthusiastic support of this project and all of the reviewers who so generously gave of their time to review the chapters in this volume. Special thanks are due to Deb Crooks, chair of the Human Biology Association Publications Committee, for her proficient management of the review process. Melissa Yanuzzi at Wiley-Blackwell and Stephanie Sakson at Toppan Best-set Premedia Limited ably oversaw the production of the book. At Wiley-Blackwell, our thanks go to our editors, Thomas Moore and Karen Chambers, and editorial assistant, Anna Ehler, for their assistance and patience.

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INTRODUCTION

Human Biology: An Evolutionary and Biocultural Perspective

SARA STINSON, BARRY BOGIN, DENNIS O'ROURKE,
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INTRODUCTION

What Are the Big Questions?

What is human biology and what do human biologists study? What constitutes the shared biology of people and other nonhuman species? What are the novel characteristics of the human species, and can the time of origin and the reasons for the evolution of these new and novel features be determined? What biological differences are there among and within living human populations, and how are these differences the product of both evolution over generations and **plasticity** during an individual's lifetime? These are several of the “big questions” in the field of human biology. This book summarizes current research aimed at answering these questions.

The major points of this chapter are the following:

- (1) Human biology is a well-defined discipline.
- (2) Human biology is founded on an evolutionary perspective.
- (3) The recognition of different types of biological adaptation, including processes of plasticity in development and behavior, is at the core of human biology.
- (4) A biocultural and cross-cultural perspective is a unifying principle of all human biological research and thinking.

BOX 1.1 DEFINITIONS OF HUMAN BIOLOGY

There is no single, all encompassing definition of “human biology.” This is due to the fact that the biology of the human species is studied from a variety of disciplines, each with its own perspective. These disciplines vary from the practical applications of clinical medicine for the treatment of human disease to studies to better understand the basic physiological pathways and mechanisms in the human body to research aimed at understanding the adaptive/evolutionary context of human biology. Here we offer a definition and a mission statement found in university catalogs and descriptions of the topics covered in three journals with human biology in their titles to provide a taste of the diversity of thought about human biology.

1. Loughborough University Human Biology Programme definition: “Human Biology is the study of humans from the cellular and individual level to the population level. Human Biologists study human anatomical structure and function and investigate the determinants of biological and behavioural variability in people, including genetic, environmental and cultural factors. Human Biologists study how the human species evolved, how the species changes over the lifespan, how humans adapt to external stressors, and how human biology and culture influence disease risk. Graduates go on to a diverse range of careers, including research, teaching, medicine or allied professions, laboratory work or graduate training schemes. The degree is unique for its emphasis on applied, individual and population level biology and the international perspective that is generated by staff research interests.”
2. Stanford University Program in Human Biology, mission statement: “The Program in Human Biology is an interschool, interdepartmental, undergraduate major. The program’s mission is to provide an interdisciplinary approach to understanding the human being from biological, behavioral, social, and cultural perspectives. The curriculum provides a broad and rigorous introduction to the biological and behavioral sciences and their interrelationships, and explores how this knowledge, in conjunction with studies in other fields, can be applied to formulate and evaluate health, environmental, and other public policies that influence human welfare.”
3. Three journals: (1) *American Journal of Human Biology*: The transdisciplinary areas covered in the journal include, but are not limited to, epidemiology, genetic variation, population biology and demography, physiology, anatomy, nutrition, growth and aging, physical performance, physical activity and fitness, ecology, and evolution, along with their interactions. (2) *Annals of Human Biology*: A journal of human population biology, reporting investigations on the nature, development, and causes of human variation, embracing the disciplines of human genetics, auxology, environmental physiology, ecology, and epidemiology. (3) *Human Biology*: A worldwide forum for state-of-the-art ideas, methods, and techniques in the field, *Human Biology* focuses on genetics in its broadest sense. Included under this rubric

are human population genetics, evolutionary and genetic demography, quantitative genetics, evolutionary biology, ancient DNA studies, biological diversity interpreted in terms of adaptation (biometry, physical anthropology), and interdisciplinary research linking biological and cultural diversity (inferred from linguistic variability, ethnological diversity, archaeological evidence, etc.).

In this chapter, we introduce the subject of this book, human biology, and the evolutionary and biocultural perspective that human biologists use in their work. While there are a number of disciplines that could (and some do) call themselves human biology because they deal with human biological characteristics, the human biology covered in this book is the discipline concerned with variation in biological traits both among and within living human populations and understanding the origin, maintenance, and implications of this variation. Human biologists investigate the genetic, environmental, and cultural determinants of biological variability in living people. They study how the human species evolved, how individual humans change over the lifespan, how humans adapt to external **stressors**, and how human biology and culture interact to shape disease risk.

Human biologists' primary interest is in biological, as opposed to behavioral, characteristics. Among the main topics that human biologists study are variation in genetic traits, disease, health, nutrition, climate responses, growth, aging, and **demography**. One important feature of human biology is its interest in *all* human populations. This interest reflects the fact that most human biologists are trained as anthropologists (especially in the United States), and like anthropologists, human biologists often study remote groups whose lives are very different from those of most of the readers of this book. For example, the authors of the chapters in this book have conducted fieldwork in Alaska, Dominica, Mexico, Guatemala, Ecuador, Peru, Bolivia, Kenya, Zaire, Egypt, Tibet, Siberia, China, The Philippines, and Samoa. But human biologists also study populations in industrialized countries, and you will see many examples of this research in this book. Human biologists study populations around the world because they are interested in understanding the effects of the many different environments with which humans must cope, and are often particularly interested in responses to severe environmental stressors such as the extreme cold in Alaska and Siberia or the very high altitudes in Peru and Bolivia.

Because human biologists frequently collect data in the field, meaning outside the laboratory or hospital setting, some traits are more feasible for them to study than others. It would be very difficult (and expensive) to conduct research using CT scans on a large portion of the world's populations. On the other hand, the instruments for measuring height and weight can be transported relatively easily to even the most remote location. As you read about human biology research, you will see the emphasis we place on developing methods that can easily be used in the field. Over the last several decades, new data collection and analysis methods have greatly increased the questions that human biologists can answer. There are now smaller instruments such as portable heart rate monitors and accelerometers to measure energy expenditure; collection methods that do not require access to electricity, such

as measuring **hormones** from saliva rather than from whole blood; and techniques that reduce the burden on the research participants, such as analysis of blood **proteins** from spots of blood, from a finger prick, dried on filter paper, rather than from blood drawn from a vein.

Human biologists study individuals, but their primary interest is in the characteristics of groups of individuals, called populations; in fact, the discipline is sometimes called human population biology (Baker 1982; Little and Haas 1989). The importance of populations to the human biologist is illustrated by comparing human biology with Western medicine (frequently called biomedicine), another discipline that is concerned with human biological traits. Both biomedical doctors and human biologists are interested in the biological characteristics of groups, but the main reason for this interest is different. In biomedicine, knowing the blood pressure of an *individual* is important mainly because it can be used to determine if the value is outside the normal clinical range, and thus if the patient is ill and in need of medical treatment. The “normal clinical range” is that found for people *within* the clinical population. In the industrialized Western nations of the United States, Canada, the European Union, Australia, and Japan, the clinical population is usually comprised of men of middle and upper **socioeconomic status**. Women, children, and ethnic minority groups are often not well represented in clinical reference values, even though there has been an effort to increase the participation of women and minorities in recent years (Department of Health and Human Services 1994; http://grants.nih.gov/grants/funding/women_min/guidelines_amended_10_2001.htm; Murthy et al. 2004). In the United States, the National Institutes of Health has explicit guidelines about including women and minorities in studies. Despite these efforts, there has been only limited improvement in the representativeness of biomedical research. Human biologists, on the other hand, are interested in knowing the average blood pressure and range of variation of *populations* to be able to compare values among and within groups, and to use these comparisons to make statements about population variation. Groups of nonindustrialized people, the hunter–gatherers, horticulturalists, pastoralists, and traditional agriculturalists studied by anthropologists/human biologists often have lower blood pressure than people in Western, industrialized nations (see Chapter 13).

Human biologists’ interest in comparison leads naturally to the questions of how variation arises, why characteristics do or do not persist in given situations, and what are the larger implications of human biological diversity. To understand how human biologists go about answering these questions, we need to look at the explanatory framework that human biologists use: an evolutionary and biocultural perspective. As Peter B. Medawar (1964), who was awarded the Nobel Prize for his work on tissue grafting and was an important theorist of aging, wrote, “Human Biology is not so much a discipline as a certain attitude of mind. . . .”

EVOLUTIONARY PERSPECTIVE

Human biologists need to account for biological change over time as well as the distribution of traits in space. As a result, human biologists—like most other biological scientists—use the synthetic theory of evolution as their primary explanatory framework.

What do we mean by the “synthetic” theory of evolution? This term refers simply to the fact that the modern theory of evolution is a synthesis of Darwinian theory (Charles Darwin, 1809–1882, published *Origin of Species* in 1859) and the science of genetics. Darwinian theory revolves around the principles of **natural selection**. At its simplest, Darwin’s theory has four basic tenets: (1) More organisms are produced than can survive; (2) organisms within a species vary in their traits; (3) some of this variation is heritable; and (4) variants best suited to the environment survive to be represented in the next generation. Mendelian genetics (Gregor Mendel, 1822–1884, proposed that inherited traits are discrete particles) provided a plausible explanation of how variation is inherited. Molecular biology and **cytogenetics** of the 20th century clarified how variation arises at the level of the deoxyribonucleic acid (**DNA**) molecule (genetics is explained in more detail in Chapter 3). Another way to explain natural selection using the language of genetics would be (1) changes in DNA can produce phenotypic changes that are subject to natural selection; (2) **phenotypes** best suited to the environment are most likely to survive and reproduce; (3) phenotypes with greater reproductive success leave more of their **genes** to the next generation; and (4) a change in **allele** frequencies from one generation to the next is defined as evolution.

Natural selection is central to human biology because changing environments over time, as well as the diversity of environments experienced by contemporaneous populations, challenge phenotypes leading to differential reproductive success of their **genotypes**. The classic example of natural selection leading to human variation is that of falciparum malaria and hemoglobin S, the protein responsible for sickle-cell disease. Populations experiencing high levels of falciparum malaria (the most deadly form of malaria) have high frequencies of the hemoglobin S allele because **heterozygotes** have an advantage in **endemic** malarial environments. Individuals with a genotype of one hemoglobin A (the most common or “normal” hemoglobin allele) and one hemoglobin S allele (AS genotype) have increased resistance to falciparum malaria and do not suffer the often fatal effects of the sickle-cell disease that occur in **homozygotes** for hemoglobin S. In populations without falciparum malaria, there is no advantage to the hemoglobin S allele, which, without medical treatment, is usually lethal to children with the homozygous SS genotype. If these children die before reproducing, then both S alleles are lost to the population and the frequency of the S allele declines over time in the population. Diversity in responses to climate extremes (see Chapter 6) and diet (see Chapter 7) provide other well-supported examples of the action of natural selection in producing human variation.

Natural selection results in adaptation. The type of adaptation that results from natural selection is called a **genetic adaptation** because the differential reproductive success that is the basis of natural selection causes changes in the frequency of alleles. As we will see below, there are other types of adaptations as well (see Fig. 1.1). By adaptation we mean a beneficial adjustment to the environment. To be considered adaptive, the benefits of the trait must be greater than its costs, but that does not mean that adaptations are always totally without cost. Hemoglobin S in malarial environments is an excellent example of this. While having the hemoglobin S allele is beneficial overall because heterozygotes have a reproductive advantage, hemoglobin S also has a cost as a result of early **mortality** from sickle-cell disease in those who inherit an S allele from each parent (SS homozygotes). Sickle cell also

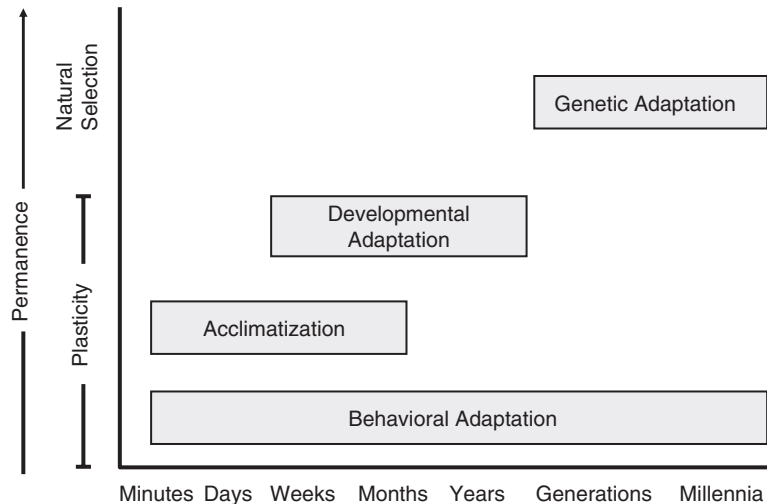


Figure 1.1 Modes of adaptation showing the different timescales at which different types of adaptations occur. Acclimatizations and developmental adaptations occur during the life-time as a result of plasticity, and can take from minutes to years to occur. Biological plasticity can involve physiological, morphological, and epigenetic changes. Humans also exhibit a high degree of behavioral plasticity, which can lead to adaptations over the short or long term. Genetic adaptations occur over generations as a result of natural selection. Adapted from a figure created by Jodi Lyons and Cynthia Beall, which was adapted from Gluckman et al. (2009b) and Thomas (1975).

illustrates that most traits are only adaptive in particular environments: Available evidence suggests that the S allele is advantageous only where there is falciparum malaria.

With a few exceptions, it has been difficult to demonstrate unequivocally the operation of natural selection in humans. At the molecular level, there are now techniques for inferring whether selection has acted on a DNA sequence (Harris and Meyer 2006), and as discussed in Chapter 6, evidence for selection has been found for a number of genes affecting high-altitude adaptation. But for most of our phenotypic traits, genes interact with each other and with the environment, so the correspondence between genotype and phenotype is not one to one (Kimura 1979). In addition, often no easily measurable relationship exists between either genotype or phenotype and reproductive success. The long generation time of humans makes us a difficult species in which to document differential survival and reproduction (or differential contributions of genes to the next generation). The difference in the number of offspring between high-altitude Tibetan women estimated to have different oxygen saturation genes is one of the rare cases in which we have come close to measuring differences in reproductive success (see Chapter 6), but much of human biological research uses other, more **proximate** indicators of probable adaptive success (health, growth, work capacity, etc.).

Natural selection is frequently considered the most important mechanism of evolution, although there is no universal agreement on this point. (Sewall Wright [1982], for example, argued for a prominent role for **stochastic** gene changes, meaning random changes in allele frequencies in populations of small **effective** size.) Regardless of which side of this debate one favors, it is important to remember that there are forces other than natural selection that lead to allele frequency change over time. It is generally accepted that four basic mechanisms can change the frequency of alleles and genotypes within a population: natural selection, **mutation**, **genetic drift**, and **gene flow**. (These forces of evolution are described in more detail in Chapter 4.)

Mutation is the ultimate source of genetic variation, through the alteration of **bases** in the DNA molecule. Mutation provides the raw material on which natural selection can operate. Because mutations arise by chance, different mutations are likely to occur in different populations, and this can be a cause of population variation. Random occurrence of different mutations is one possible explanation for why the genes conferring the ability to digest the milk sugar **lactose** in adulthood are not the same in all populations (see Chapter 7) or why the mechanisms of adaptation to high altitude are not identical in Himalayan and Andean populations (see Chapter 6).

Genetic drift refers to stochastic changes in allele frequencies, such as the one person with a particular allele being eaten by a predator or killed in a motor accident. Random change is likely to have larger effects in small isolated populations, where a given allele may be introduced and retained (or eliminated) by chance. In small populations, the loss of an individual and his or her genes could significantly reduce the overall genetic variability for the next generation. Genetic drift also operates in large populations, but its effects are so small as to be effectively unnoticeable. Because humans lived in small populations for most of our evolutionary history, genetic drift was likely a much more important cause of evolution in the past than it is today.

Gene flow is the exchange of genetic material between populations through the processes of **migration** and mating. In human populations, mobility and intermarriage have probably always been important means of maintaining genetic diversity. Historical forces such as droughts, wars, economic alliances, international trade, and colonialism have influenced the rate and location of gene exchange. Since the 19th century, global travel and population contact have undoubtedly increased rates of gene flow and thus are important mechanisms of evolution.

Mutations alone are too rare to cause perceptible changes in allele frequencies, but the frequencies of new mutations can be greatly affected by stochastic processes such as genetic drift and, as noted above, enhanced or eliminated by natural selection. On the other hand, both genetic drift and gene flow alone can cause noticeable changes in allele frequencies within populations, and thus can cause genetic variation among populations as well. It is important to remember that genetic differences among populations need not be adaptations resulting from natural selection, but can be the result of genetic drift or gene flow. A trait can also be found in a particular environment because it is the by-product of an adaptive characteristic, without the trait itself being an adaptation (Gould and Lewontin 1978).

Types of Adaptation

Building on work by Lasker (1969), Frisancho (1993) made an important distinction between genetic adaptation and phenotypic adjustment or plasticity. Genetic adaptations involve permanent modification at the genetic level, while phenotypic adaptations result from alterations to the phenotype during an individual's lifetime without any underlying change to the genes themselves. The “adjustment can be either temporary or permanent, acquired either through short-term or lifetime processes, and may involve physiological, structural, behavioral, or cultural changes aimed at improving the organism's functional performance in the face of environmental stresses” (Frisancho 1993, p. 4). Crucial in phenotypic adjustments is our plasticity, the ability to change in response to environmental stress. Acclimatizations and developmental and behavioral adaptations are at least as important as genetic adaptations to understanding human biological and cultural diversity.

Acclimatization refers to changes during the lifetime of an organism that reduce the harmful effects of naturally occurring environmental factors such as climate, nutrient imbalance, or disease. An excellent example of acclimatization is the tanning that occurs in response to exposure to the sun's **ultraviolet radiation** (UVR). By increasing the skin's **melanin** content, tanning provides some protection against skin damage due to UVR (see Chapter 6 for further discussion of tanning). As is obvious from observing light-skinned individuals after lengthy sun exposure without the benefit of sunscreen, there is a genetic basis to the ability to tan such that some individuals tan much more readily after UVR exposure than do others (who may burn). But regardless of genetic propensity to tan, tanning only occurs with exposure to UVR. As is the case for genetic adaptation, phenotypic changes are typically adaptive under specific environmental conditions. Tanning also illustrates that many acclimatizations are reversible: Tans fade when winter comes and UVR exposure is reduced.

Acclimatizations may occur during the period of growth, in which case they are called **developmental adaptations** or **developmental acclimatizations**. Because they involve changes in the way the body grows, the phenotypic changes in developmental adaptations are usually permanent once growth stops. Many of the traits that cause increases in oxygen transport in high-altitude populations, such as increases in lung size, are the result of developmental adaptation. Responses to high altitude illustrate some of the complications in clearly separating different types of adaptation. Although developmental adaptations to high altitude only occur in individuals who grow up well above sea level, long-resident populations at high altitude may have a genetically determined greater ability to undergo these developmental adaptations than do sea level populations (see Chapter 6 for further discussion).

An area of human biological research related to developmental acclimatization is the Developmental Origins of Health and Disease (DOHaD) (Kuzawa and Quinn 2009). A large body of research indicates that poor fetal growth is associated with increased risk of adult chronic diseases such as diabetes, heart disease, and **hypertension**. This connection is frequently explained using a developmental acclimatization model: Prenatal **undernutrition** results in infants with lower birth weights whose body systems are prepared (adapted) for continuing poor nutrition after birth. This developmental acclimatization goes awry, and adult disease occurs, when nutrition after birth is better than that experienced in utero and there is a mismatch between

prenatal and postnatal conditions. This interpretation emphasizes that developmental acclimatization can extend to the prenatal period. But researchers have also questioned the extent to which responses to prenatal conditions are adaptive. For example, is a fetus growing fewer kidney nephrons an advantageous response to undernutrition or does it reflect the inability of an undernourished fetus to grow that predisposes the individual to later hypertension? Given humans' long **life span**, one can also ask to what extent we are likely to have evolved an adaptive mechanism that assumes that environmental conditions experienced prenatally will be good predictors of environmental conditions later in life. DOHaD is now a burgeoning research area in both basic and clinical sciences (<http://www.mrc.soton.ac.uk/dohad/>), and there is a range of experimental models for investigating the underlying biological mechanisms. The DOHaD approach is further discussed in Chapters 11–13.

Habituation is the gradual reduction of response to repeated stimulation or the perception of stimulation. The ability to “tune out” urban noise after repeated or constant exposure is an example of habituation. Whereas phenotypic plasticity has been widely studied in human biology, habituation as a response has not.

We are now beginning to understand some of the mechanisms that lead to variation in phenotypic expression; one of the best known is called **epigenetics**. Epigenetic expression in the phenotype is a potentially heritable change in biology or behavior. But such a change does not alter DNA sequence, rather it changes the way that the DNA is regulated. Some epigenetic mechanisms are DNA methylation, histone acetylation, and micro **RNA** interference (see Chapter 11, Fig. 11.2). These mechanisms have effects on gene activation and inactivation; for example, methylation inactivates or represses gene expression. Epigenetic mechanisms may be activated by exposure to temperature extremes, exposure to disease, excess or lack of dietary factors, and many behavioral practices including physical activity, smoking, and alcohol consumption. Epigenetics is a very active area of research, with considerable overlap with DOHaD research, and is further discussed in Chapters 6, 11, and 12.

Although humans are capable of a wide variety of adaptive biological responses, much of what makes us such a flexible and adaptable species is the array of behavioral and cultural responses that we use. Some of these responses, such as language or the technology that permits clothing and heated dwellings in cold climates, seem obviously adaptive and can be called **cultural** or **behavioral adaptations**. However, other types of behavior, such as marriage patterns or cultural rules for food preparation, probably need to be investigated before we can say that they have functional significance or reduce environmental stress. To a certain extent, it is artificial to make a strict division between biological and behavioral adaptations because many behavioral/cultural adaptations are, or are in part, psychological/emotional adaptations with a neurobiological basis that can undergo evolution.

Long-Term Evolutionary Change

Human biology is very much concerned with **microevolution**, or changes in the genetic makeup of human populations. Because they deal with a single species, parts of evolutionary theory dealing with the evolution of new species, **macroevolution** and **speciation**, have received less attention, and, unlike paleontologists, human biologists are less concerned with the actual mechanisms that produce new species.

But human biologists are interested in long-term evolutionary changes, especially in how the traits they study in living human populations evolved in our **hominin** ancestors and how we compare in these traits to our primate relatives. Many of our biological characteristics reflect our primate ancestry, so for example, we have a long period of growth, large brains for our body size, and an omnivorous diet. But humans also differ from other primates, and human biologists want to understand when and why humans evolved traits that set them apart from other primates, such as our reliance on a more nutrient-dense diet than other primates of our body size (see Chapter 7) or our novel stages of growth, such as **childhood** and **adolescence** (see Chapter 11).

Life History Theory

The ways in which evolutionary theory addresses how the life cycle evolves play a major role in human biology because much of human biology concerns aspects of the human life cycle. **Life history** theory is the study of the evolution and function of life stages and behaviors related to these stages (Stearns 1992; Hawkes and Paine 2006):

The life history of a species may be defined as the evolutionary adaptations used to allocate limited resources and energy toward growth, maintenance, reproduction, raising offspring to independence, and avoiding death. Life history patterns of species are often a series of trade-offs between growth versus reproduction, quantity versus quality of offspring, and other biological possibilities given the limited time and resources available to all living things. (Bogin 2009)

Biological anthropologists and human biologists have long been interested in how human growth, **development**, **senescence**, and aging differ from that of other apes, our closest **phylogenetic** relatives, other nonhuman primates, and mammals. It is easy to document these differences, such as altricial offspring, slow and prolonged growth including childhood and adolescence stages, late start to reproduction, **menopause**, survival into the eighth and ninth decades, and maximum life span over 122 years (Crews and Bogin 2010). Determining the evolutionary forces that produced these and other aspects of life history has not been as easy. Human life history evolution is discussed further in Chapters 11 and 13.

BIOCULTURAL PERSPECTIVE

Humans are a peculiar species of mammal: bipedal, omnivorous, relatively hairless, massively **encephalized**, intensely social, and reliant on complex learned behavior for survival. We are genetically diverse, although less so than many other species of mammals (Wise et al. 1997; Jensen-Seaman et al. 2001; Kaessmann et al. 2001). Behaviorally, we are extremely diverse. Individuals communicate by using thousands of different languages, are organized into societies with widely varying structures, and solve environmental problems with myriad technological solutions. Thus, humans are a species with a highly developed capacity for symbolic thought and representation; environmental manipulation; and invention, learning, and appreciation of social facts. In short, humans have culture, a system of socially learned

behavior and belief. While other animals may have something that could be called culture (Janson and Smith 2003), no one contests that humans have elaborated culture to a greater extent than any other animal, particularly in the realm of language and symbolic thought.

These human peculiarities have ramifications for how we approach human biology. Any understanding of human biology requires that we attend to the fact that humans are cultural beings. Human biologists therefore rely heavily on a biocultural perspective. This approach recognizes that human biology interacts with culture and can only be understood in light of culture—culture both influences our environment and affects how we respond to that environment.

Culture can be considered a part of the human package of adaptive strategies, but it can also be a source of change in that both human culture and human biology require continuous flexibility and adaptability in order for humans to survive. There are numerous examples of the ways in which culture shapes the environments to which humans must adapt. The classic cases are the clearing of forests for horticulture establishing conditions for natural selection for hemoglobin S (Livingstone 1958) and the domestication of cattle and other milk-producing animals initiating natural selection for the persistence into adulthood of the ability to digest the sugar in milk (see Chapter 7). Looking at contemporary events, the ability to quickly travel the globe by air has increased the speed with which **infectious disease** can spread (see Chapter 9), reductions in physical activity as a result of technological and economic changes are probably a key cause of worldwide increases in rates of obesity (see Chapters 7, 8, and 12), employment can be an important source of stress (see Chapter 10), and food shortages due to the seasonal nature of human agricultural systems, economic and political inequality, and civil disturbances and war, cause disruptions in female ovarian function (see Chapter 15). Humans respond biologically to all of these biocultural environmental circumstances, though, as will be discussed further below, whether these responses can always be considered adaptations is debated.

Culture also plays a major role in determining how humans respond to environmental challenges. Cultural norms and traditions encode information for dealing with environmental challenges, but they also limit the available options for dealing with new environments. Your culture provides information about how to make or where to buy clothing, but it also tells you that not all possible ways of covering the body are acceptable (cardboard may keep off the rain, but it is not usually considered clothing in the context of European-American culture).

The examples below illustrate some of the complexities in fully comprehending the interaction of culture and human biology. While human biologists recognize the importance of culture as it affects human biology, measuring cultural factors and achieving a complete biocultural understanding is frequently more difficult than measuring biological characteristics (Dufour 2006).

Poverty

Because human biologists are interested in all human populations, many of the populations they study live under conditions of poverty. Understanding the effects of poverty on human biology and how poverty causes these effects are thus important questions (see Chapters 7, 10, and 12 for examples). While at first glance it might seem

that poverty is a simple concept—the poor have limited monetary and material possessions—in fact poverty is complex (Dufour 2006). There is not one poverty, but many different types of poverty. What it means to be poor in the United States or another high-income country is very different from what it means to be poor in a low-income country. In the former case, poor children are likely to have clean drinking water and indoor plumbing, while in the latter they likely will not. In most high-income countries, there is universal health care (but not in the United States) and most of the poor have an adequate quantity of food (but not all, see <http://www.ers.usda.gov/Briefing/FoodSecurity/>), although the food may not be of optimal nutritional value. For the poor in low-income countries, there is usually very limited access to biomedical health care and there may be chronic or seasonal food shortages.

From the descriptions above, one would surmise that the biological effects of poverty are more severe in low- than in high-income countries. While this is true overall (Wagstaff 2002), it has long been observed that there are health measures that do not fit this expectation, such as the fact that life expectancy in Costa Rica is about equal to that in the United States despite the higher average income in the United States (Marmot 2005). In part, this may be the result of greater emphasis on social welfare programs in the former country, but there is also evidence that factors other than purely material causes may be at play in terms of how poverty affects human biology. Many studies have found that health measures are worse in countries or regions with greater income inequality, that is, in areas with a larger range in income between the richest and the poorest (Wilkinson and Pickett 2006). This suggests a psychological dimension to poverty, such that part of being poor is *feeling* poor relative to others, no matter what your material standard of living. Or as the anthropologist Marshall Sahlins (2004, p. 37) said, “Poverty is not a certain small amount of goods (but) . . . a relation between people . . . a social status . . . an invidious distinction between classes. . . .”

The multifaceted nature of poverty means that human biologists need to consider multiple dimensions to grasp poverty’s effects. The material aspects of poverty, such as income, possessions, education, and occupation, describe only part of what it means to be poor. Many of the effects of poverty result from the interaction of material poverty with the symbolic belief system. Without knowing that it is culturally important to have beef in the main meal, it would be hard to understand why low-income women in Cali, Colombia, have cow’s hoof or cheek as part of their midday meal and why they feel humiliation in not being able to afford a more “acceptable” cut of meat (Dufour 2006). Knowing the importance of the U.S. Thanksgiving holiday meal and that the meal should contain certain foods makes sense of the observation that a low-income woman in New York state began months in advance buying one item a week for the holiday meal because she knew she would not have the money to buy all of the symbolically important foods at once (Fitchen 1988).

Even the seemingly more straightforward material aspects of poverty need to be examined in cultural context—the Western definition of what it means to “work” is not universal (Dufour 2006) and the possessions that confer status differ around the world. The Maya people of Guatemala, for example, are traditional farmers and have very little money and few material possessions. Even so, families will expend a relatively large amount of money to sponsor religious rituals through a system of social organization called *cofradias* (Chance and Taylor 1985; Rojas Lima 1986).

Doing so serves important theological and cosmological functions that maintain the order of the universe and helps to assure a good harvest of corn and other foods. Good harvests are vital for the health of the Maya people. Sponsorship also raises the social status of the family within the local community, but may force the family into debt, which may have negative consequences for family health.

A full biocultural approach requires a detailed understanding of the culture in order to be able to appreciate the social and symbolic meanings of behaviors, relationships, and material objects and from this identify the factors that are most likely to affect human biology (Dressler 1995). From this understanding can come greater insights into the pathways through which environmental factors affect human biology (see Fig. 1.2 for one model of the risks related to health, growth, and school achievement for children living in poverty in the United States).

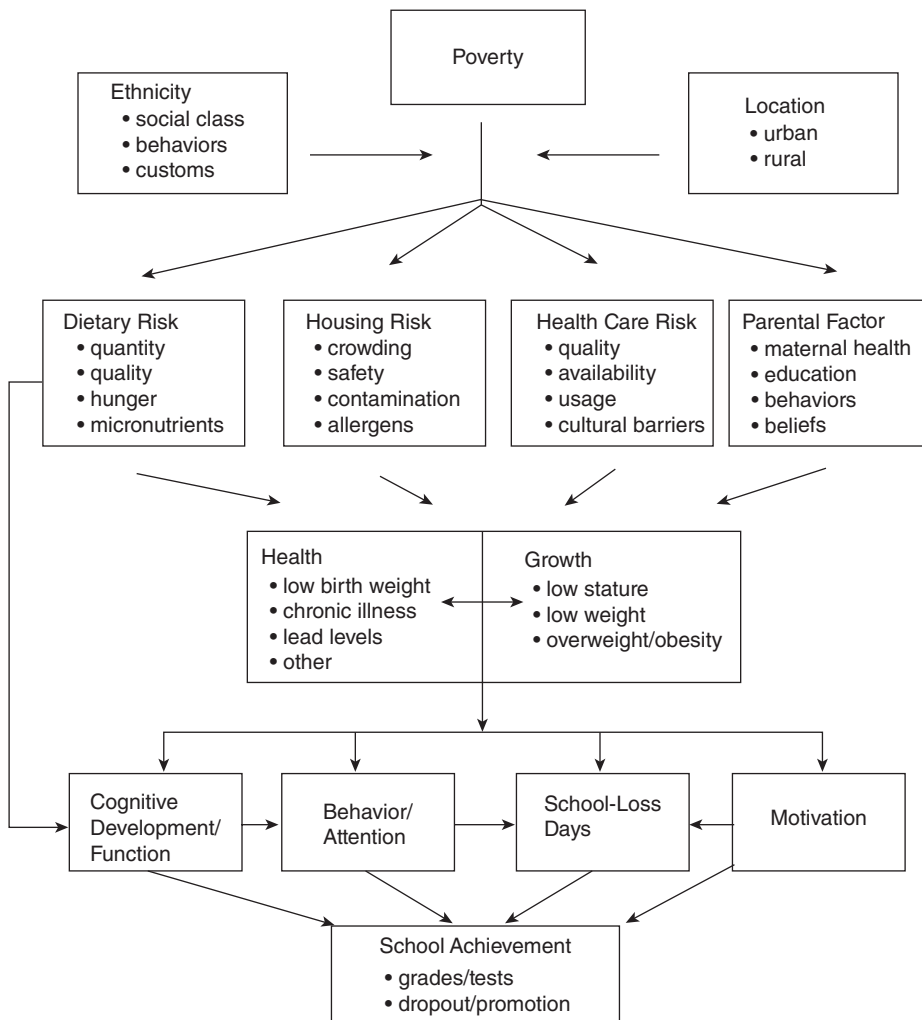


Figure 1.2 Model of poverty risks showing the multiple pathways through which poverty can affect health, growth, and school achievement. From Crooks (1995).

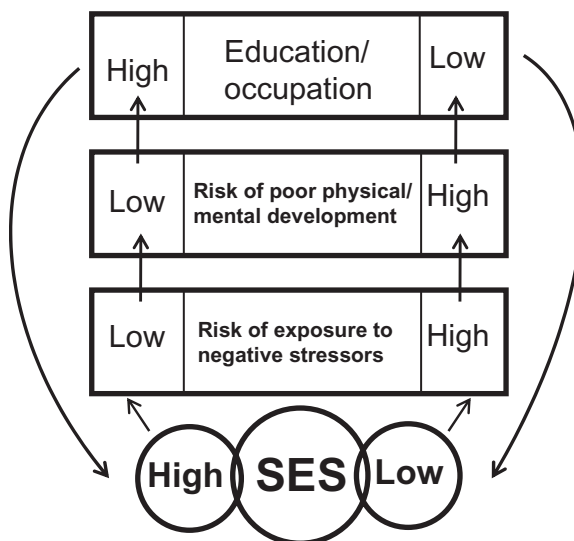


Figure 1.3 Model showing how socioeconomic status (SES) can influence exposure to environmental stressors which in turn can influence physical growth, mental development, and education and occupation. The lower risk of exposure to negative stressors associated with high SES results in more favorable health outcomes. Adapted from Schell (1997).

Political Economy

An even broader conception of poverty can come from looking at the political and economic forces that lead some populations and some individuals within populations to be poorer than others. Thus, culture cannot only produce stress but can selectively allocate impacts of stress to different portions of a population (Schell 1997, Fig. 1.3). The political-economic approach emphasizes that inequalities experienced at the local level, such as poverty, are the result of historical and current global processes. Understanding the biological effects of these inequalities requires an understanding of social relationships that reflect differences in power and that influence both exposure to stress and coping mechanisms (Goodman and Leatherman 1998). Inherent in this approach is that responses to environmental stress will vary depending on factors such as gender, class, and ethnicity, and that the really powerless (e.g., the extremely poor) may find themselves beyond their ability to adapt to their conditions, such that responses that allow them to cope in the short term have detrimental consequences for their long-term functioning and even survival. Here is another cautionary example that just because we see a response in a particular environment, that response need not be an adaptation (Bailey and Schell 2007).

The political-economic approach is exemplified by work conducted by Thomas and colleagues in the Peruvian Andes among small-scale agriculturalists and herders (Thomas et al. 1998; Leatherman 2005). Rather than taking the poverty of the region as a given, the researchers looked at the larger history of the area to understand

how the Spanish conquest followed by creation of large wool-producing haciendas, recent agrarian reform, and the penetration of cash markets into the region had created groups that differed widely in their access to necessary resources. They examined how illness affected the ability to carry out needed subsistence work, finding that poverty and poor health were mutually reinforcing. Among families with the least material resources and social support, illness of a family member could throw the family into a situation where they could not cope without substantial costs, such as planting fewer fields or taking a child out of school to provide needed labor, or even into a situation with which they could not cope, such as the need to care for a sick family member making it impossible to perform cash labor and thus having no money to buy food. At a minimum, these responses prolong poor health (by lowering food availability) or poverty (by reducing education), and one can easily imagine much more serious consequences. Here as well, the cultural belief system plays a part in the stress created by poverty because of the importance to Andean cultural identity of having land to farm and labor to exchange, items that may be lacking for the very poor.

The interplay of human biology, economics, politics, and behavior is a very active area of research today. There are several ongoing research projects across the globe. The journal *Economics & Human Biology* was inaugurated in 2003, reflecting the growth and increasing prominence of this new research area, which also appears in the *American Journal of Human Biology*, the *Annals of Human Biology*, and other peer-reviewed journals with a biocultural perspective.

Critiques of the Biocultural Approach

There are criticisms of the biocultural perspective. One criticism is that it is a cultural artifact of American anthropology, a version of the discipline that was founded on the four-field holism proposed by Franz Boas and his students (see Chapter 2). In much of the rest of the world, the teaching and practice of social anthropology, linguistics, archaeology, and biological anthropology are relegated to separate academic departments. Some critics see American anthropological holism and the biocultural perspective as artifacts from 19th century social evolutionary thought that inappropriately imposed scientific positivism upon anthropology (Segal and Yanagisako 2005). We do not find that this criticism applies to the biocultural perspective we take in this book, which is based on advances in the social sciences and biology of the past 60 years and considers human adaptations as both beneficial and harmful, often at the same time.

The biocultural perspective within human biology and, more generally, anthropology is part of the scientific exploration of the relationships between the biological and cultural nature of human beings. Human biological and behavioral characteristics, such as a large brain and what that brain can do, are part of the foundation upon which human culture is constructed. In turn, culture shapes the way people think about and act upon their world. Culture alters human biology by influencing the limits of acceptable biological and behavioral traits within a society. Heuristically, it is possible and sometimes desirable to separate biology and culture and study each alone, but for the human species, and throughout much of the evolutionary history of the hominins, biology and culture are inextricably linked in a complex web of anatomical, genetic physiological, behavioral, and social relationships.

RELATED DISCIPLINES

An evolutionary and biocultural perspective is at the core of human biology. But human biologists use concepts from and contribute research to other disciplines as well. In this section, we describe some of these related disciplines.

Biomedical Theory

We have used the term “biomedical” previously in this chapter, especially to contrast the focus on the individual of biomedicine with the focus on populations of human biology. Even with this difference in focus, a biomedical approach is central to much research in human biology today. At its simplest, biomedicine can be characterized as interested in normal anatomy, normal physiological function, and the processes that cause pathology. More complex analyses stress that the biomedical model of disease is a cultural product—a specific way of looking at the human body and its disorders—that reflects the cultural values and beliefs of industrialized societies (Rhodes 1990; Lock and Vinh-Kim 2010). Although some biomedical problems are phrased in terms of evolutionary theory, most are not. Even biomedical researchers who accept evolution as a guiding theoretical principle often ignore it in practice. Therefore, much of the work in this area appears atheoretical because the problems of interest have been identified in very practical ways, as issues in public health or clinical medicine. These health problems become of interest to human biology when they can be linked in some way to populations, that is, when their incidence, severity, or outcome varies in different identifiable human groups.

We should consider three different approaches when looking at the role of biomedicine in human biology. One is the “biomedical model” or philosophical principles that underlie medical investigation and practice. The second involves the principles and assumptions of **epidemiology**, and the third is the field of evolutionary medicine. Researchers interested in problems of human health and diseases often do not distinguish among these approaches and may use all three in any given study. Articles in human biology journals may start with a statement of the problem based on a clinical concern, proceed to methods drawn from epidemiology, and conclude with a discussion of both public health outcomes and a possible evolutionary origin of the problem.

Biomedical Model The “biomedical model” is the name given to the set of philosophical assumptions that underlie Western **allopathic medicine**, currently the dominant medical system in most industrialized countries of the world. Anthropologists and historians writing about medicine have emphasized the dualism inherent in biomedical theory. What they mean is that the body and mind are seen as separable entities; the body is part of the natural world, a bounded material entity that can be known and understood through scientific observation. Similarly, diseases are physical entities, “things” that occur or go wrong in identifiable locations in the body. This means that the body can be treated in isolation from the mind or the “spirit.”

The body can also be reduced to its parts. Systems, organs, tissues, and cells are separable parts whose function and malfunction can be studied and treated.