Chapter 1
Introduction: Evolutionary Medicine and Life History Theory

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Abstract Evolutionary medicine is a developing specialty in the biological sciences. Modern Darwinian theory posits that natural selection shapes variation in anatomy, physiology, genetics, and behavior. In this volume, we examine human health across the life span with a primary focus on life history theory - an analytical framework for understanding how organisms allocate resources to maximize reproductive success. From the standpoint of life history theory, individuals face genetic and physiological trade-offs to optimize investment in reproductive and other priorities at different stages of the life course. Trade-offs can be reflected in variation in nutritional and social status, fertility, disease risk, mortality - and other parameters conventionally thought of as "health" variables. In evolutionary terms, reproduction is the most important capacity organisms possess, since it is the means for passing genes on to the next generation. For long-lived primates, like humans, adaption to a given environment is reflected in the number of healthy, potentially reproductive offspring produced. Reproduction is costly, and timing of reproduction can have major effects on the health and mortality of both sexes over the life course. This volume brings together intellectual perspectives of biological anthropologists and evolutionary biologists from developmental biology, reproductive ecology and physiology, demography, immunology, and the biology of aging. Our aim is to showcase diverse ways in which emerging styles of evolutionary analysis can enrich our perspectives on medicine and public health. In this first chapter, we introduce basic concepts from human evolutionary biology and bioanthropology that are used throughout the volume.

To Peter T. Ellison: with appreciation from colleagues, collaborators, and former students

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1.1 Introduction

Evolutionary medicine and evolutionary public health are rapidly developing areas of biological science. (Williams and Nesse 1991; Nesse and Williams 1996; Stearns and Koella 2008; Jasienska 2013; Stearns and Medzhitov 2015) Although the term "Darwinian medicine" (later replaced by "evolutionary medicine") was first proposed in 1991 by George Williams and Randolph Nesse, an evolutionary approach to human health began much earlier in the history of science. Charles Darwin's grandfather, Erasmus, is cited as one of the first physicians to propose in the eighteenth century a connection between nature and human health. Trevathan and colleagues (1999) have provided an excellent review of the history of evolutionary medicine.

Long before the field of evolutionary medicine became recognized, many human biologists and biological anthropologists based their ideas and explanations of research findings on the principles of evolutionary theory (Ellison 2003). One of the most dominant avenues of research in the field of human biology has been the study of human variation and an emphasis on the richness of differences in anatomy, physiology, genetics, and behavior among individuals. These differences are not classified as either "normal" or "pathological" as they are in the medical field, but instead are viewed as the result of evolutionary processes.

The Arc of Life Evolution and Health over the Life Course showcases ways in which research conducted by biological anthropologists can enrich our understanding of variation in human health. This book looks at human health from the evolutionary perspective with particular focus on life history theory (Stearns 1992). (Roff 2002) Life history theory, a part of evolutionary theory, provides an explanatory framework for understanding how organisms allocate their time and energy in ways that maximize reproductive success. Given that resources are limited, individuals face trade-offs in terms of allocating resources to different stages of the life course, such as when to enter the stage of reproductive maturation or embark upon the first birth. *The Arc of Life* examines the consequences of life history trade-offs, a fundamental principle of evolutionary biology, on various aspects of human health in both sexes across the life cycle.

1.2 Brief Overview of Life History Theory

In evolutionary terms, the ability to reproduce is the most important capacity living organisms possess, allowing for passing genes on to the next generations. For animals that reproduce more than once, like many mammals, reproductive effort involves investment in multiple breeding episodes over the life course. For long-lived primates, like humans, successful adaption to a given set of environmental circumstances is measured in terms of lifetime reproductive success or the number of healthy, potentially reproductive offspring produced relative to the success of other individuals in the population.

Reproduction is costly for humans and other long-lived primates. Not only does reproductive effort involve pregnancy and lactation, it may also include long-term provisioning of mates or nurturing offspring long past weaning. A variety of factors contribute to lifetime reproductive success in humans and nonhuman primates, including the timing of birth, maturation, and spacing of reproductive episodes, the amount of energy invested in procuring mates and producing offspring, and the energetic expenditures and risks involved in sustaining pregnancy, producing milk, and other forms of offspring nurture and care. The resources needed for reproduction may be in short supply or available only seasonally. Longer reproductive life spans also necessitate maintaining healthy bodies and nonreproductive structures between breeding periods over the long haul, as well as obtaining adequate nutrition to support reproductive organs and offspring during the demands of breeding. Complex social networks and learning systems often must be negotiated or mastered. Reproductive individuals can incur significant risks in the form of predation, competition with conspecifics, physiological stress, exposure to diseases or accident, or the loss of energy stores vital for future health and reproductive investment.

The trajectory of the life span—the timing of maturation, births, and deaths—is referred to by evolutionary biologists as the *life history*. Rates of birth and mortality (*vital rates*), in turn, are referred to as *life history traits*. Evolutionary theory predicts that these demographic variables represent key aspects of an animal's phenotype that have been shaped by natural selection and contribute to lifetime reproductive success, just as other key phenotypic characteristics contribute to an individual's evolutionary success relative to others in a population. Natural selection is expected to produce organisms with the most successful adaptive "strategies" or complex sets of trade-offs among all of the benefits, costs, and risks associated with reproduction and associated phenomena. Life history trade-offs can be extremely complex and difficult to measure directly, particularly in human or other primate populations, since physiological measurements and experimental manipulations are difficult to carry out.

Some of the physiological structures, hormones, and growth factors necessary for reproduction in mammals—mammary glands, gonads, and sex steroid hormones like estrogens, progesterone, and testosterone—carry special physiological risks (e.g., an increased risk of cancer), as well as providing obvious reproductive benefits. Traits that provide developmental or reproductive benefits early in life may become liabilities later on and may contribute to the aging process (Finch and Rose 1995; Finch 2007; Cohen and Holmes 2014; Williams 1957). While natural selection is expected to optimize reproductive traits and factors during the reproductive life span, no direct evolutionary benefits accrue by surviving or remaining healthy past the period in which reproduction is possible. Traits are only adaptive insofar as they contribute to lifetime reproductive success, synonymous with Darwinian fitness. Variation in the human reproductive life span itself, therefore, reflects past natural selection as well as shorter-term responses to evolutionary change in response to novel environments.

1.3 Human and Primate Life History and Reproductive Strategies

In general, primates are relatively large, long-lived mammals with big brains and complex social behavior. Humans are longer lived than our closest primate relatives, the chimpanzees and gorillas, and other mammals of similar body size. Modern humans in industrialized countries can now live up to 30 years or more past the peak reproductive years. Humans also have a long reproductive life span characterized by large investment in each offspring, with females generally investing more than males. As in the great apes, reproduction is costly energetically and pregnancy and childbirth relatively risky. Females must make trade-offs between the number of offspring produced and the quality of care provided. For example, women with high parity often have poorer health and shorter life spans.

Investment in an unsuccessful reproductive episode is also costly in terms of lost alternative reproductive opportunities. The seasonal timing of reproduction can be critical in terms of the availability of mates or food, as can the timing in terms of the life course: very young and very old women, for example, are not as successful on average at conceiving or bringing a pregnancy to term. Males, on the other hand, may incur their biggest challenges in establishing mating relationships and obtaining access to fertile, receptive females.

Primate reproductive patterns are expected to vary with environmental conditions and population variables (including population density). Reproductive variation can take the form of adaptive behavioral, developmental, or physiological responses to environmental cues (*phenotypic plasticity*)—all limited by the genetic constraints of the population. When environmental variation exceeds the ability of animals to respond adaptively within phenotypic norms, natural selection (in the form of mortality or reproductive failure) will act to produce changes in gene frequencies and, with these, new phenotypic norms.

1.4 Cultural and Epidemiological Shift

Over the past two centuries, cultural and technological change has occurred more rapidly than at any previous time in the history of the human species (Boyd and Silk 2009). Since the Industrial Revolution in the mid-1800s, mortality rates at all phases of the human life cycle have declined. In industrialized countries like the United States, people are living on average 30 years longer than they did in 1900. With the use of reliable contraceptives, childbirth and parenting are often delayed until significantly later in life, and fertility rates are much lower than ever before.

These modern shifts in the human life history pattern are primarily the result of cultural, rather than evolutionary, change. People today live longer than our ancestors because modern sewage disposal, clean water, and the widespread availability of medical care lessen the susceptibility to infectious disease and death from accidents. Famine and warfare are less widespread now than other times in human history. Most people do not have to worry about dying of tetanus, an attack by wild animals, or exposure to the elements. While some significant genetic and phenotypic change accompanying biological evolution has undoubtedly occurred during this period as well, cultural change has generally outpaced the rate of evolutionary change.

1.5 Health in Evolutionary Perspective

Natural selection has shaped human anatomy and physiology to maximize reproductive success or Darwinian fitness, not to maximize health (or "physical fitness") over the entire life course. From the evolutionary point of view, it is important for an organism to be healthy only insofar as good health contributes to an increased ability to pass genes on to the next generations. Any trait that increases reproductive success will be promoted by natural selection even if having the trait contributes to faster aging or poor health at older ages. The following example illustrates the principle: good nutrition for girls during childhood leads to an earlier age at menarche, even though an earlier age at menarche is a significant health risk. Women who mature relatively early have a higher risk of breast cancer. Nonetheless, they also have a longer reproductive life span, which may lead to higher lifetime reproductive success. In adult women, good nutrition also leads to increased levels of reproductive hormones. Although this is beneficial for fertility, lifetime exposure to high levels of reproductive hormones increases the risk of breast cancer. Similarly, in adult men, good nutrition leads to increased levels of the reproductive hormone testosterone. Again, this is beneficial for mate competition and reproductive success, but also increases the risk of prostate cancer. Furthermore, a single gene often encodes multiple traits, which may have antagonistic effects on health. Such antagonistic genetic pleiotropy is often responsible for good health and an increased ability to reproduce at a young age but, at the same time, for increased susceptibility to health problems at older ages.

Evolutionary medicine points out that the human body is vulnerable to health problems such as chronic disease (heart disease, cancer, and diabetes) and diverse medical conditions such as myopia, skeletal and joint degeneration, and infertility for two main reasons: (1) the "mismatch" between ancient genes and modern environments given the rapid acquisition of novel diets and lifestyles, as well as a mismatch on a shorter timescale between the prenatal environment and the adult environment, and (2) inherent design "flaws" in the human body arising from the inevitable evolutionary trade-offs involved in maximizing lifetime reproductive success.

1.6 Contributions from Biological Anthropology

The Arc of Life Evolution and Health over the Life Course brings together biological anthropologists with expertise in the areas of developmental biology, reproductive ecology and physiology, demography, immunology, and senescence. Biological anthropologists tend to gear their research toward understanding not only the fitness consequences of life history trade-offs (infant mortality, pregnancy outcome, lifetime reproductive success) but also the physiological and sociocultural processes responsible for their regulation. Biological anthropologists also tend to rely heavily on both cross-cultural comparisons involving traditional or non-Western societies and cross-species comparisons in order to understand natural human variation, especially in the context of potential adaptation versus pathology. The collected volume presented here aims to illustrate the diverse ways in which biological anthropologists contribute to and further advance the field of evolutionary medicine and public health.

On a final note, the coeditors chose to title this book *The Arc of Life* as a tribute to Peter T. Ellison by referencing one of the chapters from *On Fertile Ground*. Most of the authors included in this volume were influenced by Peter's ideas and research over the decades. Peter Ellison's work in the area of human reproductive ecology established one of the most insightful applications of evolutionary theory to the intersections between biological anthropology, physiology, and human health. His innovative approach has extended to all stages of human life history and brought new understanding to many of the subdisciplines within the field of human evolutionary biology. Peter's work continues to inspire new generations of researchers in both the laboratory and field in ways that inform about human health.

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