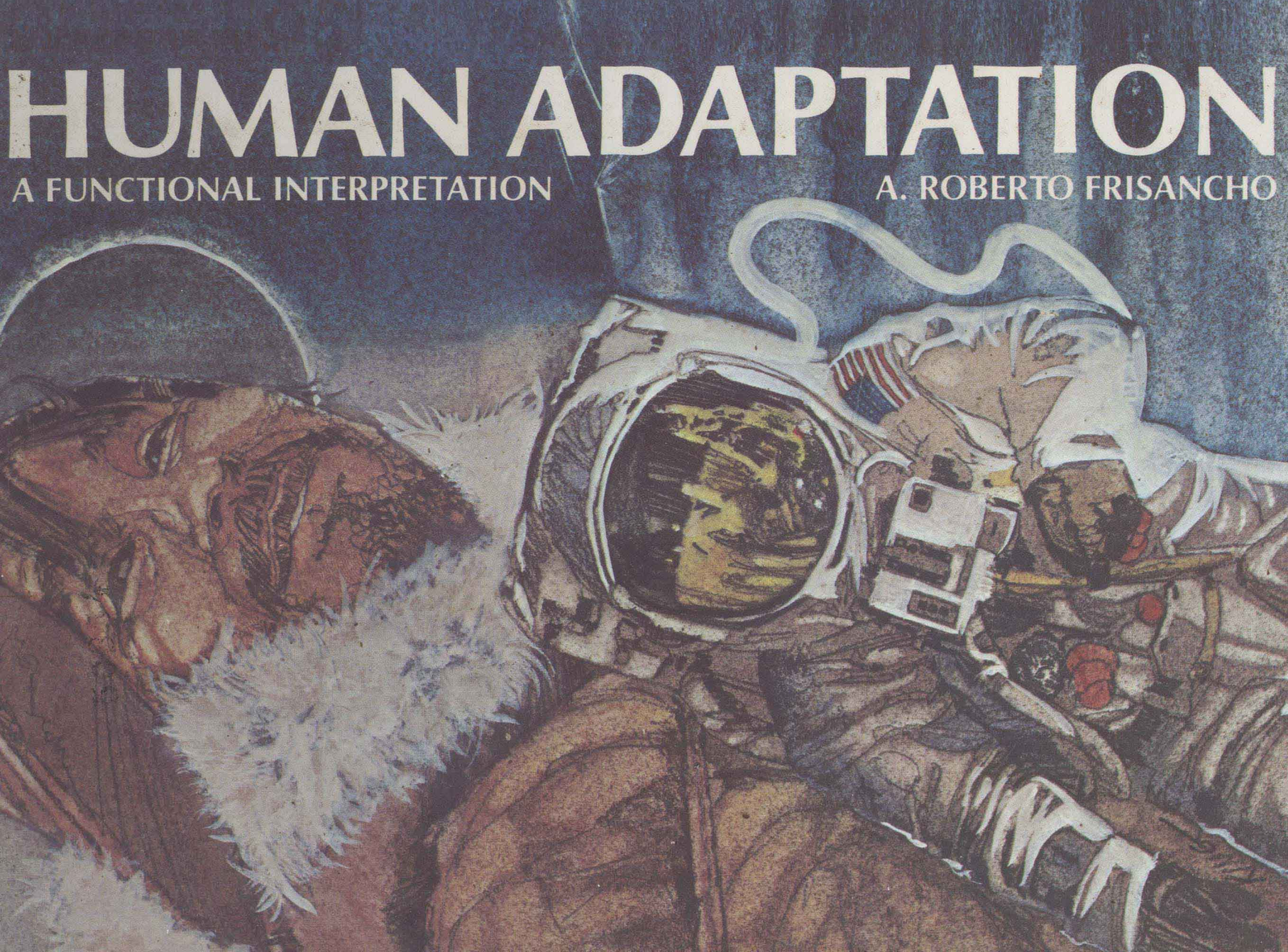
# HUMAN ADAPTATION

## A FUNCTIONAL INTERPRETATION

A. ROBERTO FRISANCHO



# HUMAN ADAPTATION

## A functional interpretation

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IN MEMORY OF

*my father* **Augusto**

AND DEDICATED TO

*my mother* **Rebeca**

*my wife* **Hedy** and

*my sons* **Roberto Javier** and **Juan Carlos**

# Preface

In recent years increased interest in the interaction between environmental conditions and the adaptive capacity of humans has led physiologists, biologists, and physical anthropologists to study the effects of climatic factors such as heat, cold, and humidity, as well as high-altitude hypoxia, solar radiation, undernutrition, and overnutrition on an organism's cellular, biochemical, and morphological functioning during both developmental and adult states. Results of these investigations have been published in specialized research articles or symposia. The goal of this book is to integrate such scattered and specialized knowledge into a single work that evaluates human adaptation from a physiological and anthropological perspective.

This book evaluates the short- and long-term responses that enable humans to function normally under the stress of heat, cold, solar radiation, high-altitude hypoxia, and undernutrition. In addition, because of their importance and influence on the well-being of humans and to show the interaction between technological adaptation and biological function, the effects of Westernization of dietary habits on the pattern of disease are briefly discussed.

Because this book is addressed to students of several disciplines and to facilitate understanding of the mechanisms of human adaptation to environmental stress, major topics are always preceded by either a chapter or section outlining initial responses observed in laboratory studies with humans and experimental animals. Emphasis is also given to the short adaptive mechanisms that enable an organism to acclimate itself to a given environmental stress. Subsequently, the long-term adaptive mechanisms that enable humans to acclimatize themselves to natural, stressful environmental conditions are discussed.

Throughout the book emphasis is given to the effects of environmental stress and the adaptive responses that an organism makes during its growth and development. For example, current

evidence suggests that population differences in adaptation to the stresses of heat, cold, and high-altitude hypoxia result in part from adaptations made during growth and development. In some cases the evidence is only suggestive, and I hope that the postulated hypotheses will stimulate researchers to prove or disprove them. If further research is so motivated, my efforts will have been worthwhile.

I would like to acknowledge my indebtedness to Professors Paul T. Baker and Thelma S. Baker of the Department of Anthropology of Pennsylvania State University, whose guidance, teaching, and friendship have been a major influence throughout my graduate training and professional life. Discussions with my colleagues of the University of Michigan have been of great benefit. My thanks to Professors Loring C. Brace, George J. Brewer, Stanley M. Garn, Frank P. Livingstone, Robert E. Moyers, Roy Rappaport, and Arthur Vander. Nello Pace, Professor Emeritus of Physiology at the University of California, Berkeley, Professor Elsworth R. Buskirk, Director of the Laboratory for Human Performance at Pennsylvania State University, and Joel M. Hanna, Associate Professor of Physiology at the University of Hawaii at Manoa all provided prepublication reviews of the manuscript, and their numerous recommendations have been most helpful.

I especially thank my Peruvian colleagues Drs. Roger Guerra-Garcia, Carlos Monge, Emilo Picon-Reategui, Cesar Reynafarje, and Tulio Velasquez of the Institute of High Altitude Studies and Institute of Andean Biology of the University of San Marcos and the University of Cayetano Heredia for their invaluable assistance and cooperation in my studies of high-altitude adaptation.

Many persons contributed to the preparation of this book. I wish to express a deep appreciation to all for their assistance. Special thanks are extended to my coresearcher and former graduate student of the Department of Anthropology of the University of Michigan, Jane E. Klayman, who from the onset of this work helped me industriously. Theryl Schessler, a former graduate student of Biological Anthropology, patiently traced all the line drawings and illustrations. I am grateful to the secretarial staff of the Center for Human Growth and Development of the University of Michigan, and I especially thank Rosanne Arnowitz, June Bixler, Barbara Nesbit, Margaret Owen, and Carol Thompson.

**A. Roberto Frisancho**

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## DEFINITIONS

Although the term *adaptation* has been widely used by biologists, social scientists, and laymen, there is no general agreement as to its meaning. Part of this difficulty is because humans adjust to their environment through a complex set of interrelationships between themselves and their physical, biological, and social environment. Consequently, both scientists and laymen use the term adaptation to indicate a multiplicity of physiological, psychological, social, and genetic characteristics. For example, among geneticists the term refers to genetic adaptation, implying that natural selection is involved[1-12]; in this context, it refers specifically to populations and not individuals. However, most nongeneticists apply the term adaptation to both individuals and populations.[13-33]

The concept of adaptation cannot be reduced to a single definition without gross oversimplification. Throughout this book the term adaptation is used in the broad generic sense of functional adaptation, and it is applied to all levels of biological organization from individuals to populations. A basic premise of this approach is that adaptation is a process whereby the organism has attained a beneficial adjustment to the environment.[1-34] This 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. If environmental stresses are conducive to differential mortality and fertility, then adaptive changes may become established in the population through changes in genetic composition and thus attain a level of genetic adaptation. In this context functional adaptation, along with cultural and genetic adaptation, is viewed as part of a continuum in an adaptive process that enables individuals and populations to maintain both internal and external environmental homeostasis. Therefore the concept of adaptation is applicable to all levels of biological organization from unicellular organisms to the largest mammals and from individuals to populations. This broad use of the concept of adaptation is justified not only in theory but also because it is currently applied to all areas of human endeavor so that no discipline can claim priority or exclusivity in the use of the term.[20] In this chapter the various forms of adaptation will be defined, and their relationship to each other, as well as their applicability to the study of human adaptation to environmental stress, will be discussed.

### Functional adaptation

Functional adaptation involves changes in organ system function, histology, morphology, biochemical composition, anatomical relationships, and body composition, either independently or integrated in the organism as a whole. These changes can occur through acclimatization, acclimation, or habituation.

**Acclimatization.** Acclimatization refers to changes occurring within the lifetime of an organism that reduce the strain caused by stressful changes in the natural climate or by complex environmental stresses.[21,22,34] If the adaptive traits are acquired during the growth period of the organism, the process is referred to as either *developmental adaptation* or *developmental acclimatization*.[23,32]

**Acclimation.** Acclimation refers to the adaptive biological changes that occur in response to a single experimentally induced stress[21,22] rather than to multiple stresses as occurs in acclimatization. As with acclimatization, changes occurring during the process of growth may also be referred to as developmental acclimation.[32]

**Habituation.** Habituation implies a gradual

reduction of responses to, or perception of, repeated stimulation.[21,22] By extension, habituation refers to the diminution of normal neural responses, for example, the decrease of sensations such as pain. Such changes can be generalized for the whole organism (general habituation) or can be specific for a given part of the organism (specific habituation). Habituation necessarily depends on learning and conditioning, which enable the organism to transfer an existing response to a new stimulus. The extent to which these nonphysiological responses are important in maintaining homeostasis depends on the severity of environmental stress. For example, with severe cold stress or low oxygen availability, failure to respond physiologically may endanger the well-being and survival of the organism.

**Acclimatization vs acclimation.** Studies on acclimatization are done with reference to both major environmental stresses and several secondary, related stresses. For example, any difference in the physiological and structural characteristics of subjects prior to and after residence in a tropical environment are interpreted as a result of acclimatization to heat stress. In addition, because tropical climates are also associated with nutritional and disease stresses, individual or population differences in function and structure may also be related to these factors. On the other hand, in studies of acclimation any possible differences are easily attributed to the major stress to which the experimental subject has been exposed in the laboratory. For understanding the basic physiological processes of adaptation, studies on acclimation are certainly better than those of acclimatization. However, since all organisms are never exposed to a single stress but instead to multiple stresses, a more realistic approach is that of studying acclimatization responses. Thus, both studies on acclimation and acclimatization are essential for understanding the processes whereby the organism adapts to a given environmental condition. This rationale becomes even more important when the aim is to understand the mechanisms whereby humans adapt to a given climatic area, since humans in a given area are not only exposed to diverse stresses but have also modified the nature and intensity of these stresses as well as created new stresses for themselves and for generations to come.

### Cultural and technological adaptation

Cultural adaptation refers to the nonbiological responses of the individual or population to modify or ameliorate an environmental stress. As such, cultural adaptation is an important mechanism that facilitates human biological adaptation. It may be said that cultural adaptation both during contemporary times and in evolutionary perspective represents humanity's most important tool. It is through cultural adaptation that humans have been able to survive and colonize far into the zones of extreme environmental conditions. Human beings have adapted to cold environments by inventing fire and clothing, building houses, and harnessing new sources of energy. The construction of houses, use of clothing in diverse climates, certain behavioral patterns, and work habits represent biological and cultural adaptations to climatic stress. The development of medicine from its primitive manifestations to its high levels in the present era and the increase of energy production associated with agricultural and industrial revolutions are representative of human cultural adaptation to the physical environment.

Culture and technology have facilitated biological adaptation, but they have also created and continue to create new stressful conditions that require new adaptive responses. A modification of one environmental condition may result in the change

of another. Such a change may eventually result in the creation of a new stressful condition (Chapter 14). A classic example of such an interaction of culture and biology is the development of malaria. In West Africa malaria became hyperendemic when the *Anopheles gambiae* mosquito, the major vector of malaria, was propagated because of the development of agriculture in the tropical rain forest of West Africa.[7] It was in response to this new stress that the adaptive qualities of the abnormal hemoglobins, such as sickle cell and thalassemia, became important to the survival of man in tropical climates. In the same manner, advances in the medical sciences have successfully reduced infant and adult mortality to the extent that the world population is growing at an explosive rate, and unless world food resources are increased, the twenty-first century will witness a world famine. Western technology, although upgrading living standards, has also created a polluted environment that may become unfit for good health and life. If this process continues unchecked, environmental pollution will eventually become another selective force to which humans must adapt through biological or cultural processes or face extinction. Therefore, the ability to adapt to the unforseeable threats of the future remains an indispensable condition of survival and biological success.[29] Adaptation to the world of today may be incompatible with survival in the world of tomorrow unless humans learn to adjust their cultural and biological capacities.

### Genetic adaptation

Genetic adaptation refers to specific heritable characteristics that favor tolerance and survival of an individual or a population in a particular total environment. A given biological trait is considered genetic when it is unique to the individual or population and when it can be shown that it is acquired through biological inheritance. A genetic adaptation becomes established through the action of natural selection, the central theme of Darwinian evolution. Natural selection refers to the mechanisms whereby the genotypes of those individuals showing the greatest adaptation or "fitness" (leaving the most descendants through reduced mortality and increased fertility) will be perpetuated, and those less adapted to the environment will contribute fewer genes to the population gene pool. Natural selection favors the features of an organism that bring it into a more efficient relationship with its environment. Those gene combinations fostering the best-adapted phenotypes will be "selected for," and inferior genotypes will be eliminated. The selective forces for humans as for other mammals, include the sum total of factors in the natural environment. All the natural conditions, such as hot and cold climates and oxygen-poor environments, are potential selective forces. Food is a selective force by its own abundance, eliminating those susceptible to obesity and cardiac failures, or by its very scarcity, favoring smaller size and slower growth. So is disease a powerful selective agent, favoring in each generation those with better immunity. The natural world is full of forces that make some individuals, and by inference some populations, better adapted than others because no two individuals or populations have the same capacity of adaptation. The maladapted population will tend to have lower fertility and/or higher mortality than that of the adapted population.

The capacity for adaptation (adaptability) to environmental stress varies between populations and even between individuals. The fitness of an individual or population is determined by its total adaptation to the environment—genetic, physiological, and be-

havioral (or cultural). Fitness in genetic terms includes more than just the ability to survive and reproduce in a given environment; it must include the capacity for future survival in future environments. The long-range fitness of a population depends on its genetic stability and variability. The greater the adaptation, the longer the individual or population will survive and the greater the advantage in leaving progeny resembling the parents. In a fixed environment, all characteristics could be under rigid genetic control with maximum adaptation to the environment. On the other hand, in a changing environment a certain amount of variability is necessary to ensure that the population will survive environmental change. This requirement for variability can be fulfilled either genetically or phenotypically or both. In most populations a compromise exists between the production of a variety of genotypes and individual flexibility. Extinct populations are those which were unable to meet the challenges of new conditions. Thus, contemporary fitness requires both genetic uniformity and genetic variability.

Therefore contemporary adaptation of human beings is both the result of their past and their present adaptability. It is this capacity to adapt that enables them to be in a dynamic equilibrium in their biological niche. It is the nature of the living organism to be part of an ecosystem whereby it modifies the environment and, in turn, is also affected by such modification. The maintenance of this dynamic equilibrium represents homeostasis, which, in essence, reflects the ability to survive in varying environments.[20,29] The ecosystem is the fundamental biological entity—the living individual satisfying its needs in a dynamic relation to its habitat. In Darwinian terms, the ecosystem is the setting for the struggle for existence, efficiency and survival are the measures of fitness, and natural selection is the process underlying all products.[29]

## PURPOSE OF ADAPTATION: HOMEOSTASIS

An environmental stress is defined as any condition that disturbs the normal functioning of the organism. Such interference eventually causes a disturbance of internal homeostasis. *Homeostasis* means the ability of the organism to maintain a stable internal environment despite diverse, disruptive, external environmental influences.[29] On a functional level, all adaptive responses of the organism or the individual are made to restore internal homeostasis. These controls operate in a hierarchy at all levels of biological organization, from a single biochemical pathway, to the mitochondria of a cell, to cells organized into tissues, tissues into organs and systems of organs, to entire organisms.

The maintenance of dynamic equilibrium constitutes the major objective of the various adaptive responses made by organisms. The necessity for the maintenance of homeostasis results from the fact that cellular functions are limited to relatively small variations. For example, the chemical composition of the blood, lymph, and other body fluids varies within relatively narrow limits.

Humans living in hot or cold climates must undergo some functional adjustments to maintain thermal balance; these may comprise the rate of metabolism, avenues of heat loss, heat conservation, respiration, blood circulation, fluid and electrolyte transport, and exchange. In the same manner, persons exposed to high altitudes must adjust through physiological, chemical, and morphological mechanisms, such as increase in ventilation, increase in the oxygen-carrying capacity of the blood resulting from an increased concentration of red blood cells,

and increased ability of tissues to utilize oxygen at low pressures. Failure to activate the functional adaptive processes may result in failure to restore homeostasis, which in turn results in maladaptation of the organism and eventual incapacity of the individual.

Therefore homeostasis is a part and function of survival. The continued existence of a biological system implies that the system possesses mechanisms that enable it to maintain its identity, despite the endless pressures of environmental stresses.[29] These complementary concepts of homeostasis and adaptation are valid at all levels of biological organization. They apply to social groups as well as to unicellular or multicellular organisms.[29]

Homeostasis is a function of a dynamic interaction of feedback mechanisms whereby a given stimulus elicits a response aimed at restoring the original equilibrium. Several mathematical models of homeostasis have been proposed. In general, they show (as schematized in Fig. 1-1) that when a primary stress disturbs the homeostasis that exists between the organism and the environment, to function normally the organism must resort either to biological or cultural-technological responses. Through the biological responses, the organism overcomes the environmental stress and its physiological activities occur either at the same level as before the stress or take place at another level. For example, when faced with heat stress, the organism may simply reduce its metabolic activity so all heat-producing processes are slowed down, or may increase the activity of the heat-loss mechanisms. In either case the organism may maintain homeostasis, but the physiological processes will occur at a different set point. The attainment of full homeostasis or full functional adaptation, depending on the nature of the stress, may require short-term responses such as those acquired during acclimation or acclimatization or may require exposure during the period of growth and development as in developmental acclimatization. In theory the respective contributions of ge-

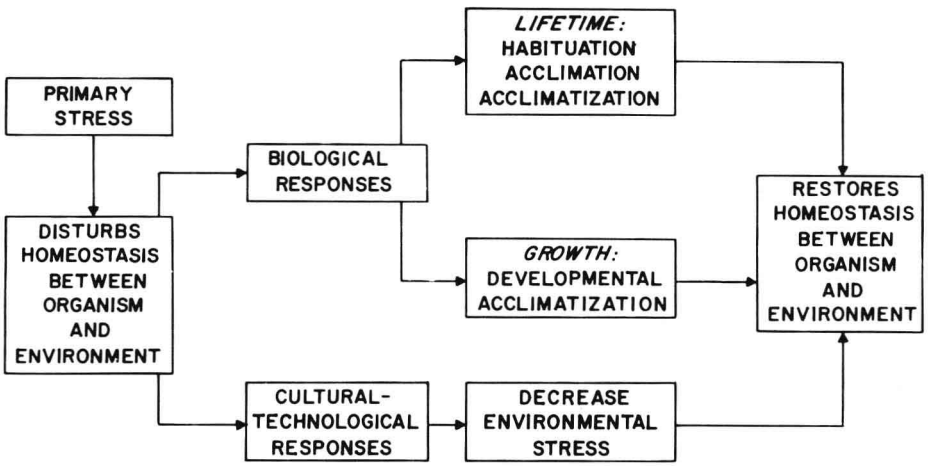


**Fig. 1-1.** Schematization of adaptation process and mechanisms that enable individual or population to maintain homeostasis in the face of primary disturbing stress.

netic and environmental factors vary with the developmental stage of the organism—the earlier the stage, the greater the influence of the environment and the greater the plasticity of the organism.[23,29,32] However, as will be shown in this book, the principle does not apply to all biological parameters; it depends on the nature of the stress, the developmental stage of the organism, the type of organism, and the particular functional process that is affected. For example, an adult individual exposed to high-altitude hypoxia through prolonged residence may attain a level of adaptation that permits normal functioning in all daily activities and as such we may consider him adapted. However, when exposed to stress that requires increased energy, such as strenuous exercise, this individual may prove to be not fully adapted. On the other hand, humans through cultural and technological adaptation may actually modify and thus decrease the nature of the environmental stresses so that a new microenvironment is created to which the organism does not need to make any physiological responses. For example, cultural and technological responses permit humans to live under extreme conditions of cold stress with the result that some of the physiological processes are not altered. However, on rare occasions humans have been able to completely avoid an environmental stress. Witness the fact that the Eskimos, despite their advanced technological adaptation to cold in their everyday hunting activities, are exposed to periods of cold stress and in response have developed biological processes that enable them to function and be adapted to their environment.

Not all responses made by the organism can be considered adaptive. Although a given response might not be adaptive per se, through its effect on another structure or function it may prove beneficial to the organism's function. Conversely, a given adaptive response may aid the organism in one function but actually have negative effects on other functions or structures. Thus, within all areas of human endeavor a given trait is considered adaptive when its beneficial effects outweigh the negative ones. In theory this is a valid assumption, but in practice, because of the relative nature of adaptation, it is quite difficult to determine the true adaptive value of a given response. Every response must be considered in the context of the environmental conditions in which the response was measured and within the perspective of the length of time of the study and the subject population.

## ADAPTATION RESEARCH

### Empirical and experimental

The study of human adaptation involves a unique combination of field and laboratory methods, whereby the knowledge of ecologists, physiologists, geneticists, and cultural and physical anthropologists is pooled in an attempt to understand the human-environment relationship. To accomplish this objective, two different but related approaches are employed. The first is the geographical method, which may be called the indirect method. The indirect, or geographical, method attempts to establish the relationship between certain morphological or physiological characteristics and an environmental parameter. For example, anthropologists on a worldwide basis have established the relationship of various morphological features to climatic variables, such as temperature and humidity.[11,12] Because of the complex nature of a given climatic variable, the geographical method does not reveal the cause for the existence of this relationship. The explanation of the observed relationship requires the second, direct or experimental, approach. The experimental method collects and analyzes precise measurable changes in humans under reproducible and controlled

experimental conditions, both in the laboratory and in the field. These conditions are the result of measurable environmental factors, which are generally of a chemical, physical, or biological nature and usually enable us to predict the qualitative and quantitative responses to each particular environment. The experimental approach requires a thorough understanding of the physiological and anatomical properties of the organism and the environmental parameters. It is a method designed to test a special theory, hypothesis, or assumption derived from the geographical, or indirect, method. In other words, research in adaptation requires the application of the geographical and experimental methods. The indirect method provides the pathway for experimental research. These methods permit the student of human adaptation to understand the mechanisms whereby a given population survives adverse environmental conditions such as heat, cold, altitude, disease, and malnutrition. The study of human adaptation is not oriented to determining biological or cultural differences among populations; the goal is to identify the sources or causes that resulted in such adaptation and differences.

### Individuals vs populations

Whatever the method employed, geographical or experimental research in human adaptation is concerned with populations, not with individuals, although the research itself is based on individuals. There are two related reasons for this.

The first is a practical consideration. Studying all members of a given population, unless its size is small enough, is too difficult to be attempted by any research team. Therefore, according to the objectives of the investigation, the research centers on a sample that is considered representative of the entire population. Based on these studies, the researchers present a picture of the population as a whole, with respect to the problem being investigated.

The second reason is a theoretical one. In the study of adaptation, we usually focus on populations rather than on individuals because it is the population that survives and perpetuates itself. In the investigation of biological evolution, the relevant population is the breeding population because it is a vehicle for the gene pool, which is the means for change and hence evolution. The study of an individual phenomenon is only a means to understand the process. The adaptation of any individual or individuals merely reflects the adaptation that has been achieved by the population of which he is a member.

## CONCLUSION

The term *adaptation* encompasses the physiological, cultural, and genetic adaptations that permit individuals and populations to adjust to the environment in which they live. These adjustments are complex, and the concept of adaptation cannot be reduced to a simple rigid definition without oversimplification. The functional approach in using the adaptation concept permits its application to all levels of biological organization from unicellular to multicellular organisms, from early embryonic to adult stages, and from individuals to populations. In this context, human biological responses to environmental stress can be considered as part of a continuous process whereby past adaptations are modified and developed to permit the organism to function and maintain equilibrium within the environment to which it is daily exposed.

The mechanisms for attaining full functional adaptation include acclimation, acclimatization, and habituation. The role played by each of these processes depends on the nature of the stress or stresses, the organ system involved, and the develop-