THE ADAPTIVE LIMITS OF HUMAN POPULATIONS*

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The biological and behavioural variation in recent human populations is explored in relation to the environmental stresses which developed during human evolution. While early hominid evolution produced a form genetically adapted to the climate and biota of the hot savannah, hominid populations from *Homo erectus* onwards adapted to an increasingly diversified combination of natural and cultural stresses. It is suggested that this diversity of stresses was a result of an interlocked process whereby populations, in adapting to new environments, created new stresses which evoked further adaptive responses. Examples of how biological and cultural adaptations created new stresses are offered. The adaptation of the Amerindians to the environment of the high Andes is reviewed to illustrate the complex biological and cultural interactive mechanisms of an environmental adaptation. While the spread of modern urban industrial society appears to be reducing the diversity of stresses, results from a study of Samoans show that the nature and intensity of biological stress encountered by modernising populations is regulated by the adaptations previously made to the traditional environment. It is concluded that the rapid changes in stress associated with modern society may well test the limits of the human adaptive capacity.

By the end of Thomas Huxley's lifetime, the idea that man's body had evolved from another animal form was accepted by the majority of biological scientists and by a fair number of individuals in the developing social sciences. There was, however, less scientific agreement as to the reasons why recent human populations differed in obvious physical traits and many theories were put forward to explain why groups of people varied so substantially in behavioural and belief systems.

Explanations for these variations remain far from adequate today. Research over the past thirty years, however, suggests that, as with other animal species, some of the population differences in both biology and behaviour are the result of adaptations to the stresses encountered in our complex environmentally mediated evolution.

In this article I will attempt briefly to illustrate (1) the stresses which shaped the basic biological characteristics of our ancestors prior to their emergence in our present sapient form; (2) the biological and cultural characteristics which allowed the human populations of the recent past to exist in a diverse set of new environmental niches; and (3) the implications of our past adaptive processes for human life in the modern world.

To attempt this, I must cope with several biological terms which do not have identical definitions across the biological disciplines and which are often used in a totally different way by social scientists. It would be tedious to define all the

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terms, but the concepts of adaptation and stress are particularly diverse in their usages so that it is essential for me to explain how I will use them.

For the purpose of this article, an adaptation is simply any biological or cultural trait which aids the biological functioning of a population in a given environment. Thus, it includes such aspects as a population's health, ability to feed itself adequately, functional capability in its physical environment and reproductive performance. This definition encompasses the more precisely defined forms of adaptation used in genetics and the adaptability responses which are denoted by such terms as acclimatisation. However, it stops short of encompassing sociocultural adjustments which do not have demonstrable effects on human biological functions. Stresses are defined as those natural or cultural environmental forces which potentially reduce the population's ability to function in a given situation.

These definitions are unlikely to please all scientists but they do make possible an account of how selected biological and cultural traits permitted recent human populations to function in their environments. Although it does not imply causality, this account does allow exact statements to be made about the past, present and future biological consequences of many population characteristics.

The sources of our adaptive capacity

The genetic sources of our basic adaptive capacity obviously do not have recent origins. Human morphology and physiology allowed even the nineteenth century taxonomist to demonstrate easily that our biological adaptations had their origins in earlier animals. Darwin's reconstruction of our general phylogenetic history remains unchallenged, as does his contention that the great apes are our nearest relatives. The palaeontological and biochemical discoveries of the present century have modified the Darwinian view in only two ways of major significance for understanding the Primate origins of our adaptations. First, recent discoveries show that the time period for hominid divergence was much longer than previously assumed (Johanson & White 1979), and second, molecular genetic research findings now suggest that, despite our apparent behavioural complexity, the genetic differences between *Homo sapiens* and other African apes may be no greater than, or perhaps even less than, the differences among the other apes (Goodman 1982). Thus, we may now conclude that, during the early stages of hominid development, there was adequate time for evolution to fine-tune our genetic structure to the environment. However, the evolutionary pace of genome replacement was probably no faster than it was for other phylogenetic lines of our common Anthropoid ancestors.

Over the relatively long period of evolution which led to *Homo erectus*, it appears that the predecessors of *erectus* occupied a uniform environmental niche. No matter which pre-*Homo erectus* fossil one picks as an ancestor, environmental stresses are similar compared to the diversity of environments in which later hominids occur. All, for example, appear to have lived in savannah or semi-arid conditions. That this affected our genetic structure is well attested to by the fact that our physiology and morphology are best adapted to a hot dry climate. Our physiological responses are much less effective in hot wet conditions and our physiological responses to cold are so ineffective that many of our sensory and motor functional abilities begin to decline when we live nude in temperatures below 20°C.

The food sources available in these tropical savannahs must also have been very similar through time, so that diet probably remained quite constant over the evolution of the pre-*Homo erectus* forms. Many biological anthropologists would not agree with this statement, since dental morphological variations among some of the early forms have been interpreted as dietary specialisations (Robinson 1963) and the upright locomotion of the early forms might be interpreted as an adaptation to hunting (Dart 1953). Nevertheless, our basic nutrient needs are similar to those of our close relative, the chimpanzee (Nicholosi & Hunt 1979), and I see no compelling reason to believe that our early predecessors were affected by any change in the kinds of food available or experienced significant alterations in their ability to obtain various types of foods.

Beyond these potential effects of climate and food, the types and persistence of other stresses become highly speculative. The absence of evidence for a significant change in technology suggests that each generation had to solve the problems of survival and reproduction with a very similar set of behaviours and tools. Scientific knowledge about these early environments and the biological characteristics of the resulting hominids is fragmentary. As a consequence I conclude only that for a very long period of human evolution adaptation to environmental stress kept our ancestors within the bounds of a savannah environment. Apart from the development of upright locomotion and slight changes in dentition, there is little evidence for substantial morphological or behavioural change during these millions of years.

It is logical to believe that a changing environment helped produce the *Homo erectus* stage of human evolution, but we do not really know what caused the development of this form. Whatever the causes, we do know that they spread into a variety of new natural environments. Fossil evidence of this hominid shows a broad geographical spread from Java to China, Europe and Africa. The geographical spread along with the fluctuating climate of the early Pleistocene must have caused not only changing stresses over time, but also much greater differential stresses on subpopulations than those encountered by their predecessors.

Over twenty years ago, Carleton Coon (1962) suggested that the various forms of fossils still generally classified as *Homo erectus* had indeed responded to their environments by developing morphological adaptations. He linked this idea to the notion that recent 'race' differences began with these adaptations. The latter part of his argument was poorly received for a variety of reasons. Perhaps because of this poor reception, very few researchers have attempted to test whether or not the morphological differences in *Homo erectus* groups can be associated with variation in environmental stress. Nevertheless, from studies of living populations, it seems highly likely that living in such diverse natural environments would produce biological variation among these hominid forms.

With an increasing rate of biological change, a series of fossil forms then appeared. For the purposes of the present analysis, their taxonomy is unimportant. However, let us assume that most of these forms contributed to the genetic and cultural repertoire of *Homo sapiens*. This stage in the process of human evolution appears to have placed populations in even more diverse and changeable natural environments than those prevailing during the *Homo erectus* stage. These fossils have not only followed the geographical spread of *Homo erectus* but have also been found in clear association with fauna and flora showing that some of the populations lived in cold steppes, others in temperate forest areas and some perhaps even in wet tropical areas. The spread into colder regions could not have occurred without the use of body covering and probably involved the use of fire for body warming. Certainly the types of foods suitable for human use must have varied in kind and distribution among the environmental niches occupied by these populations, so that they were subjected to contrasting dietary stresses, including new behavioural requirements for obtaining food.

During this period, significant variation in tools and living arrangements can be detected, suggesting that a variety of behavioural systems existed. Some of these behavioural variations may have been adaptive, others biologically stressful. One must also assume that such a variety of natural environments must have contained different disease stresses, accident stresses, etc., but how the populations adapted to them is unknown. What is certain is that these hominids survived for a long time in a much broader array of natural environments than did *Homo erectus*.

In summary, our early evolutionary history offers some interesting insights into the adaptive structure of our species, provided even limited assumptions are made. It appears that in the early period of our evolution, we developed in an environment with consistent stresses. Beginning with *Homo erectus*, the natural environmental stresses became more diversified and, for our more immediate ancestors, even more diversification occurred. Along this stream of time, the adaptive responses of hominid populations to these different environmental stresses must have led to increasing variation between them in terms of morphology, physiology and behaviour. Thus, we must have entered the *sapiens* stage with a culture and biology already substantially varied by population in response to the range of conditions prevailing in occupied environmental niches. We may have also entered this stage with a set of stressors which were changing with increasing rapidity.

Homo sapiens *and his environment*

The spread of human populations over the natural environments of the world continued at an accelerated pace after the development of *Homo sapiens*. Populations at an early stage occupied Australia, north America, and then south America. As the last glaciation waned, the high altitude plateaus of the tropical mountains were peopled and finally, as more sophisticated technologies developed, the Arctic and most islands of the world were occupied. Thus, by the time of the European exploratory voyages, only Antarctica and a few of the most remote small islands were uninhabited. The species subpopulations also lived in a diversity of culturally defined environments. Technologies varied not only in complexity, but also in specific material content. Major differences between populations also resulted from the impact of varied forms of social organisation, affecting every aspect of behaviour from division of labour to mating patterns. In some biological populations, the effect of social divisions based on class or caste was to expose the subgroups of each population to quite different environments, even within a restricted ecological niche. Thus, by the time of the ethnographic present, human populations came to live in hundreds, if not thousands, of different natural environments, each with potentially unique sets of environmental stressors. Subgroups of a single species had adapted to each of these environments at least well enough to ensure reproductive viability. This unusual accomplishment had generally been attributed to our cultural ingenuity and has often been explained as an aspect of cultural diversity (Forde 1949; Steward 1955). The next section will show, from recent studies, that the explanation is more complex, involving a combination of morphological, physiological and behavioural adaptations.

Stress and adaptation in traditional populations

The natural environmental stresses of the ethnographic present. The previous remarks have focused on the new forms of stress to which human populations were exposed by their geographical spread and increasingly differentiated cultures. In this section I will specify in somewhat more detail the nature of these stresses.

The characteristics of the natural environment provide the most obvious and most easily quantifiable stresses. For an animal genetically adapted to a tropical savannah, the physiological problems of living in other temperature regimes are enormous. As previously noted, functional capabilities are impaired outside a rather narrow range of savannah temperatures and humidities. Arctic winter conditions or icy water will kill a nude individual within minutes, while hot wet conditions significantly limit work capacity. Our species also evolved as a low altitude form, so that rapid transit to an altitude with the reduced oxygen pressure found above 3,000 meters affects brain function (McFarland 1969), and at altitudes of 6,000 meters, death is inevitable even if it may take some months to occur (Pugh 1966).

Some of the other physical environmental variations associated with our geographical spread produce less dramatic effects but can nevertheless act as significant stressors on a population. Although tropical savannahs appear to be relatively dry, the water vapour content of the air is always higher than in the extreme desert and much higher than in the cold or high altitude zones of the world. Extreme moisture variations are not lethal *per se*, but affect both our respiratory and epidermal surfaces so as to reduce our resistance to a variety of infectious diseases. Natural environmental variation in ultraviolet radiation can also act as a potential stressor. Too much ultraviolet penetration below the epithelial skin layer can damage the skin, opening the way for massive infection, while too little will reduce the ability to produce vitamin D, a frequently inadequate nutrient in human diets (Daniels *et al.* 1972). Even the variation in the physical structure of the new environments must have posed threats for an animal which evolved in the tropical savannah. Children are easily lost in a dense forest, men die in the unexpected cracks of an arctic ice pack, and people are confounded by the mirages of deserts because our visual sense has not been preconditioned to interpret these images.

The diversity of environments occupied by human populations also led to variety in biological stressors. Of these, the most important must have been infectious diseases and the altered forms of potential human foods. From the distribution of infectious diseases in the present world, one suspects that movement into colder and drier environments exposed human populations to potentially fewer infectious diseases while movement into wetter tropical environments increased their number. The massive depopulations caused by the introduction of smallpox into central Mexico at the time of the Spanish conquest (Diaz del Castillo 1956), and the depopulating effect of introducing gonorrhea into the Pacific island of Yap (Hunt 1978), show that each minor shift of human populations between environmental zones must have been fraught with disease stresses. We may likewise infer that the change of environmental niche might well have produced new stresses in the search for food. New flora were found and often resemblances to previously used foods were misleading. Thus, the highly edible cassava of the Andean slopes was similar in appearance to the poisonous cassava of the Amazon basin. The deadly nightshade of the Eastern hemisphere resembled the tomato of the Western hemisphere. Edible animal species varied in behaviour so that a successful hunting style in one environment often became useless in the next.

Cultural adaptation and stress. As is very obviously shown by the physiological characteristics of today's *Homo sapiens*, we could not have spread into all the natural environments in which we existed during the ethnographic present if it had not been for a number of behavioural modifications which may be attributed to changes in culture. Thus, the adaptation of a human population to the extreme cold of the arctic required the development of such material items as effective shelter, sophisticated clothing, and a controlled use of fire. It also required the development of new behaviour patterns and observational techniques in order to utilise these material items effectively for cold protection.

What is less obvious is that the behavioural adaptations which allowed people to live in the cold of the arctic created for them a set of biological stresses which had not existed for previous human populations. For example, insulative clothing, while effective in maintaining an adequate core body temperature, is incapable of preventing frostbite damage to the extremities of inactive adults exposed to arctic winter temperatures (Baker 1960). Thus, the clothing adaptation of the Eskimos allowed them to inhabit a new microenvironment where, for the first time, severe extremity frostbite became a significant stressor. Perhaps of equal significance, the series of cultural traits which allowed the Eskimos to live in the arctic led them into a truly unique food environment. Alone among the natural environments, it often provided virtually no sources of vegetable food and the populations had to exist for long periods on diets of only animal fat and protein. That this set of behavioural adaptations to cold helped create a set of new stresses is shown by the fact that in some Eskimo populations, life expectancies were among the lowest known in the world (Weiss 1973).

Many of the Eskimo groups must have failed in the adaptive process and became extinct. Those which survived often did so by the energetically expensive method of combining high levels of reproduction with a set of biological adaptations which raised their caloric needs.

Several other examples of how behavioural adaptations to physical environmental stresses created new biological stress can be documented. The necessary clothing for living in the cloudy temperate climates of the world appears to have created at least one new form of stress. Vitamin D deficiency, with its accompanying rachitic symptoms in children, seems to have occurred only when the combination of high latitude, frequent cloud cover, and the combined use of shelter and clothing reduced ultraviolet exposure to very low levels. In more recent times, the use of smokey fires in highland New Guinea huts for mosquito protection has created respiratory disease stress (Feachem 1977) while the soft iron pots of many African cooks stress the livers of their epicurians (Walker & Arvidsson 1953).

Perhaps the most significant of all the behavioural adaptations was food-producing. This adaptation to human food requirements allowed our immediate ancestors vastly to increase the calories available for human consumption in a wide variety of environments. More than any other previous set of cultural or biological adaptations, it allowed an increase in the number of people. In the numerical sense, food-producing was one of the most successful of adaptations. At the same time, the complex set of environmental changes associated with the development of agriculture produced a still incompletely described set of new biological stresses. At the most apparent level, the foods produced in a given agricultural system were often so restricted in particular nutrient content that a number of forms of malnutrition appeared which were unknown in hunting and gathering populations. The agricultural complexes based on root crops such as cassava, taro and potato were so deficient in protein that they required supplementation by herding, fishing or hunting and gathering (Mazess & Baker 1964; Lowenstein 1973). The maize-based system of central America was potentially thiamine deficient, while the rice-based system of east Asia was potentially Vitamin B-12 deficient. By the time the diets provided by these agricultural complexes came to be evaluated in recent years, most appear to have been balanced by supplementary food items. However, the low life expectancy of the early agriculturalists suggests that a high level of nutritional stress must have existed as these food complexes developed (Rathbun 1982).

More serious stresses, both very recent and continuing, resulted in part from growth in numbers made possible by the adoption of agriculture. The principal forms of biological stress which have been identified are new infectious diseases. The dense populations promoted, though they did not directly cause, the development of such diseases as smallpox, measles, mumps, pneumonic plague, chicken pox, malaria, and a number of others (Cockburn 1971; McNeill 1976). Of these, one of particular interest is malaria, which remains only partially controlled by modern public health practices and to which some populations have demonstrable genetic adaptations (Motulsky 1975).

Coupled with population growth, the social organisational and political changes which followed the adoption of agriculture are indeed so complex that one would find it difficult to document the variety of new potential stresses which may have arisen. I will only note that, for the first time, there also appeared in the same natural environmental settings large subdivisions in the populations which encountered sharply varying environmental stresses because they belonged to subaggregates for which we now use such terms as caste, class, elite, or even slaves and masters.

High altitude adaptation. It may be useful to describe a specific example in order to show in somewhat greater detail how the interaction of morphological, physiological and behavioural adaptive processes allowed populations to occupy new environments. The data, accumulated over the past twenty years, are sufficient to provide examples from many groups, but I will use data on the high-altitude Quechua of Peru to illustrate my case, because of my personal involvement in the research.

There is no evidence of human occupation in this region earlier than 14,000 years ago (Little 1981). Yet when the Spanish arrived in the high Andean region in the sixteenth century they found not only a dense population but also an extensive political empire. Political unrest in the Inca empire and the sophisticated weaponry of the Spanish led to an easy conquest. However, the conquistadores found the environment so biologically stressful both to themselves and to their subsistence system, that they rapidly moved their capital down to the coast and only slowly, over several centuries, partially colonised the highlands.

The stresses of the high-altitude Andean region are indeed formidable for an animal adapted to a low-altitude tropical savannah. Shortwave radiation, including ultraviolet levels, are high, the air moisture levels are much below savannah levels and annual temperature on the Andean *altiplano* averages only about 6°C. Most important of all, the partial pressure of atmospheric oxygen at 4,000 meters is only about 60 per cent. of the sea level value. For agriculturalists further problems appear, since the growing season is short in most of the high altitude areas and at altitudes of 4,000 meters and above temperatures fall below freezing at least once every month of every year. Rainfall amounts are also low in the southern Andes with a short wet season. Despite these problems, Amerindians, in the brief span of 14,000 years, had not only settled this region but had increased their population to over 6 million.

The adaptations which allowed this Amerindian colonisation and proliferation may never be completely known but the biological persistence of the original populations and the Incaic subsistence pattern found by the Spanish conquistadores have allowed some research on how this adaptive structure was built. The results suggest the following adaptations to direct physical environmental stresses (Baker & Little 1976).

1. *Increased shortwave radiation.* The relatively dark skin colour of the high Andean populations may be a genetic adaptation to high ultraviolet radiation. More certainly, the current clothing, including the use of hats by both sexes, is a protection. The responses to the potentially mutant genetic effects of high ultra shortwave radiation remain unexplored.

2. *Low vapour pressure*. The notably long, narrow noses of the highland native may be an adaptation to aridity. At least such a hypothesis is compatible with the finding that there is a strong worldwide correlation between population nose shape and vapour pressure. In addition, the particular swaddling system used for infants tends to increase the moisture content of the child's inspired air.

3. *Low atmospheric temperatures*. Unlike many groups elsewhere in the world, the high altitude Quechua appear to make little use of fire in adjusting to the cold temperatures. Instead, a layered clothing system is the primary means for keeping warm. This is supplemented in many areas by adobe house structures and behavioural patterns which reduce exposure to the quite low nighttime temperatures. In addition, the Andean native has a high extremity blood flow during exposure to moderate cold which not only keeps hands and feet warm but also facilitates oxygen release from haemoglobin. The biological basis of this high extremity blood flow is not completely clear. The magnitude of the response is too great to be explained by short-term acclimatisation. Developmental changes which increase blood flow response occur but the high Quechua response may also reflect a different genetic structure from the one underlying European and African responses to the same conditions.

4. *Reduced partial pressure of oxygen*. The stress of the low partial pressure of oxygen in the *altiplano* is potentially great, since studies on other animals and lowland human beings show it can increase abortion rates and reduce fecundity, the viability of offspring, physical growth rates and work capacity. Highland Andean natives appear to achieve lowland work capacities in spite of this stress. This achievement is partly related to biological changes during growth, which we may term developmental acclimatisation, and may also be partly related to the genetic structure of the population. However, evidence for a specific gene which enhances oxygen transmission in native highlanders is lacking. Fecundity, prenatal development and child growth rates are all adversely affected, even in high-altitude Andean natives, although in all instances the effects seem to be less than they are for lowland natives who migrate to high altitude. Despite this evidence for incomplete adaptation, fertility is currently far above the level needed for population replacement and adults are fully functional with no evidence that life expectancy is unusually affected by the low oxygen pressure.

5. *Food production stresses*. As previously noted, the number of environmental constraints on food production through agriculture and herding is great. The range of adaptations to these constraints is also too great for simple enumeration. Instead, it can be noted that, on the basis of recent practices, it appears that the adaptations effected to support the prehistoric and current populations involve the use of altitude-adapted plants and animals, a number of land use strategies, a planned sex and age distribution of labour and a number of social organisational structures which R. B. Thomas (1979) believes were essential to support the populations. In addition, he has noted, along with John Murra, that

either multiple ecozone controls or exchange systems were probably necessary to maintain the Andean populations at their pre-contact numbers.

The combination of adaptations which allowed human populations to occupy and reach high densities in the high-altitude region of the Andes was obviously successful. Nevertheless, as suggested, they also produced stresses to which the adaptations remain incomplete. From present evidence it appears that fecundity may be somewhat lowered in highland natives (Baker 1978). More certainly the number of children with pathologically low birth weights is above sea-level values while the number of children with such debilitating birth defects as *patent ductus arteriosis* is many times higher than sea-level values. Adaptations to the agricultural and pastoral constraints of high-altitude regions have also limited the potential response of the native populations. Thus, attempts to increase production through the use of technologies available from medieval agriculture or contemporary agronomy have not generally succeeded (Baker 1982).

Stress and response in modern populations

Despite the successful adaptations which allowed traditional populations such as the Andean natives to function in the natural environments of the ethnographic present, the systems were unstable and subject to rapid change. These changes occurred not only as a consequence of the new stresses created within a population but also as a consequence of stresses which occurred when the people or ideas of one population intruded on another. The potential magnitude of these stresses is shown by the often catastrophic population declines which occurred in isolated populations contacted by the voyagers and colonials of the sixteenth to nineteenth centuries. While many of the contacted populations successfully incorporated the technological adaptations of the intruding people, the new stresses they brought with them, such as diseases and discrepant values, were generally so overwhelming that recipient populations were decimated in numbers and reduced in functional capacity.

The impact of cultural and personal contact between populations from industrial urban societies and more traditional groups appears to have changed during the past fifty years. Thus, in newly contacted groups and in those with which contact has increased, people are generally living longer and are rapidly growing in numbers. Examples of these new impacts are numerous. In my experience, the Shibipo of the Peruvian tropical forest stand out since, when I was doing research with them, this group had been in contact with modern society for only a decade and already had a vastly increased fertility with a declining mortality. Throughout the world it appears that a majority of traditional populations are adopting the products of urban industrial societies, as well as Western medicine, leading to increased life expectancy and growing numbers relative to growth in the older urban industrial nations. These trends readily suggest that the process of proliferating stresses and adaptations, which began with the *Homo erectus* stage of evolution and proceeded until quite recently, may be ending with a trend towards homogenised stress and universal adaptations.

Such a scenario for the future may be possible but I should like to emphasise that the present-day integration of traditional populations into the modern urban industrial societies is not producing a uniform set of stresses or responses in the various populations. Our present study of a Polynesian population has led me to this view.

Since 1975 a group of investigators, including myself, has been examining the problems encountered by Samoans as they rapidly modify their life style from a traditional one to full participation in Western society. We began the study with the idea that we were examining this population as a representative one undergoing the processes of modernisation and that the resulting data would therefore typify the kinds of biological and, to some extent, cultural problems which traditional, isolated populations encounter when they change to a modern life style (Baker & Hanna 1981). To detect these changes we have tried to determine the biological and cultural characteristics of Samoans living in the most traditional villages of western Samoa, the capital of western Samoa, the much modified areas of American Samoa and the Samoan migrants in Hawaii and San Francisco.

As the results of these studies have accumulated, we have increasingly realised that while the biological and cultural responses of the Samoans in this process of change have some general relationship to the responses shown by other populations experiencing the transition, they are in many ways unusual. In fact, modernised Samoans are subjected to a series of new stresses which they share with only a few other populations in the world. When the reasons for this uniqueness are sought, they almost always seem to relate to the particular stresses and adaptations which Samoans underwent in settling and surviving on their home islands (Baker in press).

To exemplify the unusual responses, three biological stresses which are particularly severe for Samoans caught up in the process of modernisation can be cited. An immediate problem is the enormous weight gain shown by Samoans when they migrate to Hawaii and San Francisco or live a relatively affluent life in American Samoa (Pawson & Janes 1981). Most traditional agricultural populations increase in body weight when they change to a modern life style but the weight gain in Samoans is clearly exaggerated compared to all other recorded groups. Our current surveys show, for example, that middle-aged Samoan women average 90 kilograms in Hawaii and may average 100 kilograms in San Francisco, even though their height approximates U.S. averages. The Samoans also develop an unusually high frequency of diabetes when they adopt a modern life style. The death rate from diabetes for American Samoans is higher than any industrial nation (Crews & MacKeen 1982). Samoans in San Francisco have a much higher prevalence than either Whites or Blacks in the United States. A third instance is provided by work capacity. Thus, one study showed that the potential work capacity (as determined by maximum oxygen consumption capacity) of young Samoan migrants to Hawaii was so low that a substantial proportion of these migrants could not physiologically meet the work requirements of many of the manual occupations open to them (Greksa 1980).

These responses seem to have adaptational antecedents in Samoan prehistory. Thus, Samoans, as with many other Pacific populations, appear to have been subject to natural selective pressures which favoured individuals capable of rapid weight gain. They also developed a food production complex of coconut, taro, breadfruit, pig and fishing which was so well adapted to their volcanic islands that very little human work output was needed for maximum production. Indeed, all of our studies to date confirm that work requirements were very low in traditional Samoan society and that the levels of physical fitness were correspondingly very low (Greksa 1980).

It is probably much too soon to detect significant adaptations by the Samoans to their new stresses, but culturally they are coping with some of them by retaining their traditional system of pooling economic resources in an extended family structure. Among the most modernised of Samoans in Hawaii, there is also some evidence that they may be finding methods of controlling their weight gain and increased blood pressure (Hanna & Baker 1979). In addition, while fertility levels in traditional villages are very high, often reaching a total completed fertility of nine, the American Samoans and the Samoan migrants in Hawaii have so far maintained an average total completed fertility of about five children per woman.

The new stresses and responses of the Samoans when they entered modern society are in marked contrast to those indicated by the results of our study of what happened to high-altitude Andean natives when they migrated to the Peruvian coast (Baker & Beall 1982). In this instance, respiratory disease proved to be the major cause of death while cardiovascular disease remained unimportant. The growth rate of children increased but adult weight changed little. Birth spacing decreased and even total completed fertility rose slightly. Some of these differences in responses may have occurred because of the differences in life style between the Samoan migrants and the Peruvian migrants, but the fact remains that the types of stresses which affect traditional populations changing to more modern life styles are not uniform and we should not expect that in the immediate future the types of biological and cultural adaptations which modernising populations make will be similar.

Conclusions

In conclusion, what does our biological and cultural history suggest about our adaptive limits? To me it reveals the following.

First, the biological adaptations associated with the evolution of the hominids resulted in a proliferation of human occupied environmental niches, i.e., from forms limited to tropical savannahs with low interpopulation variability in behaviour to ones occupying most of the world's terrestrial environments with much more population behavioural diversity between populations.

Second, the altered brain functions which led to what anthropologists call culture were a major factor in our adaptations to these new environments, but our species also has a morphological and physiological lability which often results in an improved functional ability when the individual is exposed to a given stress for a period of time. Some of the improved capacities require that the entire growth period be spent in the stressful environment.

Third, the process of adaptation to new environments often resulted in cycles of new stress formation and adaptation. Some of the adaptive processes resulted in specific genetic adaptations but did not lead to speciation because of high gene flows and frequent population replacements through migration.

Finally, extremely recent trends appear to be reducing the variability in the environmental stresses to which human populations are exposed. However, the cultural and biological uniqueness of the various populations entering modern society causes each to encounter slightly different stresses when it adopts a so-called 'modern' life style. Even if all human groups were subject to uniform stress, this would not signal a slowdown in the formation of stresses which test the limits of our adaptive capacity. Indeed, developments in urban industrial society over the past century have set record rates of new stress formations followed by rapid adaptations which in turn led to still different stresses. I will not presume to suggest whether this process of change will result in extinction for the species or relative stability, but I will timorously suggest that the possibility for survival might be enhanced by retention of the variety of both biological and cultural adaptations that have characterised our evolution.

REFERENCES

Baker, P. T. 1960. Climate, culture, and evolution. *Hum. Biol.* **32**, 3–16.

——— 1978. The adaptive fitness of high-altitude populations. In *The biology of high-altitude peoples* (ed.) P. T. Baker. Cambridge: Univ. Press.

——— 1982. The central Andes: environment, biology, and economic development: a perspective. *Mount. Res. Dev.* **2** (special issue. Human population and biosphere interactions in the Central Andes (ed.) P. T. Baker), 127–40.

——— in press. Migrations, genetics, and the degenerative diseases of South Pacific islanders. In *Migration and mobility* (ed.) A. J. Boyce. London: Taylor & Francis.

——— & C. M. Beall 1982. The biology and health of Andean migrants: a case study in south central Peru. *Mount. Res. Dev.* **2** (special issue. Human population and biosphere interactions in the Central Andes (ed.) P. T. Baker), 81–95.

——— & J. M. Hanna 1981. Modernization and the biological fitness of Samoans: a progress report on a research program. In *Migration, adaptation and health in the Pacific* (eds) C. Fleming & I. Prior. Wellington: Epidemiology Unit, Wellington Hospital.

——— & M. A. Little (eds) 1976. *Man in the Andes: a multidisciplinary study of high-altitude Quechua.* Stroudsburg, Pennsylvania: Dowden, Hutchinson & Ross.

Cockburn, T. A. 1971. Infectious diseases in ancient populations. *Curr. Anthrop.* **12**, 45–62.

Coon, C. S. 1962. *The origin of races.* New York: Alfred A. Knopf.

Crews, D. E. & P. C. MacKeen 1982. Mortality related to cardiovascular disease and diabetes mellitus in a modernizing population. *Social Sci. Med.* **16**, 175–81.

Daniels, F., P. W. Post & B. E. Johnson 1972. Theories of the role of pigment in the evolution of human races. In *Pigmentation: its genesis and biological control* (ed.) V. Riley. New York: Appleton-Century-Crofts.

Dart, R. A. 1953. The predatory transition from ape to man. *Int. anthrop. ling. Rev.* **1**, 201–18.

Diaz del Castillo, B. 1956. *The discovery and conquest of Mexico, 1517–1521.* New York: Grove Press.

Feachem, R. G. A. 1977. Environmental health engineering as human ecology: An example from New Guinea. In *Subsistence and survival: rural ecology in the Pacific* (ed.) T. P. Bayliss-Smith. London: Academic Press.

Forde, C. D. 1949. *Habitat, economy and society.* London: Methuen.

Goodman, M. 1982. Biomolecular evidence on human origins from the standpoint of Darwinian theory. *Hum. Biol.* **54**, 247–64.

Greksa, L. P. 1980. Work requirements and work capabilities in a modernizing Samoan population. Thesis, Pennsylvania State University.

Hanna, J. M. & P. T. Baker 1979. Biocultural correlates to the blood pressure of Samoan migrants in Hawaii. *Hum. Biol.* **51**, 481–97.

Hunt, E. E., Jr 1978. Ecological frameworks and hypothesis testing in medical anthropology. In *Health and the human conditions: perspectives on medical anthropology* (eds) M. H. Logan & E. E. Hunt, Jr. North Scituate, Massachusetts: Duxbury Press.

Johanson, D. L. & T. D. White 1979. A systematic assessment of early African hominids. *Science* **203**, 321–30.

Little, M. A. 1981. Human populations in the Andes: the human science basis for research planning. *Mount. Res. Dev.* **1**, 145–70.

Lowenstein, F. W. 1973. Some considerations of biological adaptation by aboriginal man to the tropical rain forest. In *Tropical forest ecosystems in Africa and South America* (eds) B. J. Meggers, E. S. Ayensu & D. W. Duckworth. Washington, D.C.: Smithsonian Institution Press.

McFarland, R. A. 1969. Review of the experimental findings in sensory and mental functions at high altitude. In *Biomedicine of high terrestrial elevations* (ed.) A. H. Hegnauer. Natick, Massachusetts: U.S. Army Research Institute of Environmental Medicine.

McNeill, W. H. 1976. *Plagues and people.* New York: Anchor Press/Doubleday.

Mazess, R. B. & P. T. Baker 1964. Diet of Quechua Indians living at high altitude: Nuñoa, Peru. *Am. J. clin. Nutr.* **15**, 341–51.

Motulsky, A. G. 1975. G6PD and abnormal hemoglobin polymorphism: evidence regarding malarial selection. In *The role of natural selection in human evolution* (ed.) F. M. Salzano. Amsterdam: North Holland Publishing Company.

Nicolosi, R. J. & R. D. Hunt 1979. Dietary allowances for nutrients in nonhuman primates. In *Primates in nutritional research* (ed.) K. C. Hayes. New York: Academic Press.

Pawson, I. G. & C. Janes 1981. Massive obesity in a migrant Samoan population. *Am. J. public Health* **71**, 508–13.

Pugh, L. G. C. 1966. A programme for physiological studies of high-altitude peoples. In *The biology of human adaptability* (eds) P. T. Baker & J. S. Weiner. Oxford: Clarendon Press.

Rathbun, T. A. 1982. Morphological affinities and demography of metal-age Southwest Asian populations. *Am. J. phys. Anthrop.* **59**, 47–60.

Robinson, J. T. 1963. Adaptive radiation in the australopithecines and the origin of man. In *African ecology and human evolution* (eds.) F. C. Howell and F. Bourliere. *Viking Fd Publ. Anthrop.* **36**, 385–416.

Steward, J. H. 1955. *Theory of culture change.* Urbana, Illinois: Univ. of Illinois Press.

Thomas, R. B. 1979. Effects of change on high mountain human adaptive patterns. In *High altitude geoecology* (ed.) P. J. Webber, Boulder, Colorado: Westview Press.

Walker, A. R. P. & U. B. Arvidsson 1953. Iron 'overload' in the South African Bantu. *Trans. R. Soc. trop. Med. Hyg.* **47**, 536–48.

Weiss, K. M. 1973. *Demographic models for anthropology* (Mem. Soc. Am. Archaeol. **27**).