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Human Adaptation to High Altitude

Biocultural mechanisms of adaptation are explored in a population native to the high Andes.

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Stretching along western South America from Colombia to Chile lies a large section of the Andean plateau, or *Altiplano*, which rises above 2500 meters (about 8250 feet) (Fig. 1). This area is suitable for human habitation up to the permanent snow line, which is generally above 5300 meters (17,590 feet). There are now more than 10 million people living in this zone, and the historical and archeological records indicate that it has been densely populated for a long time. Indeed, before Europeans arrived, the Inca empire, which had its center in this zone, formed one of the two major civilizations of the Western Hemisphere and, in A.D. 1500, probably contained about 40 percent of the total population of the hemisphere.

With such a history, one would assume this to be an ideal environment for man and the development of his culture. Yet, in point of fact, modern man from a sea-level environment ("sea-level man") finds this one of the world's more uncomfortable and difficult environments. The historical records show that such was the case even in the 1500's, when the Spanish complained of the "thinness of the air," moved their capital from the highlands to the coast, and reported that, in the high mining areas, the production of a live child by Spanish parents was a rare, almost unique, phenomenon (*1*). Today this environmental zone remains the last major cultural and biological center for the American Indian. The population has an extremely low admixture of genes from European peoples and virtually none from African peoples. The few cities are Hispanicized, but the rural areas retain a culture which, in most aspects, antedates the arrival of the Spaniards.

It would be far too simplistic to suggest that this unique history is explicable entirely on the basis of the effects of altitude on sea-level man. Yet, there is sound scientific evidence that all sea-level men suffer characteristic discomfort at high altitudes, the degree of discomfort depending upon the altitude. There is evidence, also, of long-term or permanent reduction in their maximum work capacity if they remain at these altitudes, and evidence that they undergo a number of physiological changes, such as rises in hemoglobin concentrations and in pulmonary arterial pressure. In a few individuals the initial symptoms develop into acute pulmonary edema, which may be fatal if untreated. On the basis of less complete scientific evidence, other apparent changes are found for sea-level man at high altitudes: temporary reduction in fertility, reduction in the ability of the female to carry a fetus to term, and a high mortality of newborn infants (*2, 3*).

With these problems in mind, a group of scientists from Pennsylvania State University, in collaboration with members of the Instituto de Biología Andina of Peru, decided to investigate the biological and cultural characteristics of an ecologically stable Peruvian Quechua population living in traditional fashion at a high altitude. We chose for study the most stable population known to us at the highest location reasonably accessible. It was hoped that some insight could be gained into the nature of this quite obviously successful and unusual example of human adaptation. In this article I review some of the results available from this continuing study.

The general problem may be defined by three questions: (i) What are the unique environmental stresses to which the population has adapted? (ii) How has the population adapted culturally and biologically to these stresses? (iii) How did the adaptive structures become established in the population?

Our basic method of study, in attempting to answer these questions, was a combination of ecological comparisons and experimental analysis.

The Study Population

The population chosen for study lives in the political district of Nuñoa, in the department of Puno in southern Peru. In 1961 the district had a population of 7750 and an area of about 1600 square kilometers. Geographically, the district is formed of two major diverging river valleys, flat and several kilometers broad in the lower parts but branching and narrow above. These valleys are surrounded by steep-sided mountains. In the lower reaches of the valley the minimum altitude is 4000 meters; the higher parts of some valleys reach above 4800 meters. The intervening mountains rise, in some parts, to slightly above 5500 meters.

The climatic conditions of the district are being studied from weather stations on the valley floors and on the mountain sides at different altitudes. From present records, the pattern seems fairly clear. The lower valley floor appears to have an average annual temperature of about 8°C with a variation of only about 2°C from January, the warmest month, to June, the coldest. This is much less than the diurnal variation, which averages about

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17°C. The seasonal variation in temperature is due almost entirely to cloud cover associated with the wet season. Some snow and rain fall in all 12 months, but significant precipitation begins around October, reaches its peak in January, and ends in April. Since the diurnal variation is high, some frost occurs even in the wet months. Mean temperatures fall in proportion to increases in altitude (by about 1°C per 100 meters), but, because of the sink effect in the valleys, minimum temperatures on the valley floors are usually somewhat lower than those on the lower mountain sides.

Except for two small areas of slow-growing conifers, almost all of the district is grassland. Because of the existing climatic and floral conditions, herding has become the dominant economic activity. Alpaca, llama, sheep, and cattle, in that order, are the major domestic animals. Agriculture is limited to the cultivation of frost-resistant subsistence crops, such as "bitter" potatoes, *quinoa*, and *cañihua* (species of genus *Chenopodium*). Even these crops can be grown only on the lower mountain sides and in limited areas on the lower valley floors. In recent years, crop yields have been very low because of drought, but they are low even in good years.

A single town, also called Nuñoa, lies within the district and contains about one-fourth of the district's population; the other three-fourths live in a few native-owned settlements called *allyus*, or on large ranches or *haciendas*, which are frequently owned by absentee landlords. The social structure may be loosely described as being made up of three social classes: a small (less than 1 percent) upper class, whose members are called *mestizos*; a larger intermediate class of individuals called *cholos*; and the Indians, or *indígenas*, who constitute over 95 percent of the population. Membership in a given social class is, of course, based on a number of factors, but the primary ones are degree of westernization and wealth. Race appears to be a rather secondary factor, despite the racial connotations of the class designations: *mestizos*, of mixed race; *cholos*, transitional; *indígenas*, indigenous inhabitants. Biologically the population is almost entirely of Indian derivation.

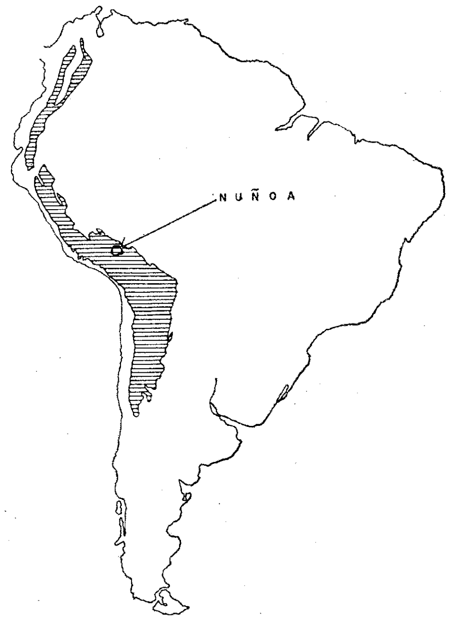


Fig. 1. The high-altitude areas of South America and the location of Nuñoa. Shading indicates altitude of 2500 meters (8200 feet) or more.

By Western economic and medical-service standards, this district would be considered very poor. If we exclude the *mestizo*, we find per capita income to be probably below $200 per year. The only medical treatment available in the district is that provided by a first-aid post. The upper class has access to a hospital in a neighboring district. Yet repeated surveys suggest that the diet is adequate, and that death rates are normal, or below normal, for peasant communities lacking modern medicine. Indeed, this population must be viewed as being one nearly in ecological balance with its technology and its physical environment.

Superficial archeological surveys reveal that the central town predated the Spanish conquest, and suggest that the district population has been fairly stable for at least 800 or 900 years.

From this general survey of the Nuñoa population and its environs we have concluded that the unusual environmental stresses experienced by this population are hypoxia and cold; other stresses, more common to peasant groups in general, which the Nuñoa population experiences are specific infectious diseases, the problems of living in an acculturating society, and, possibly, nutritional deficiencies.

Hypoxia

At elevations such as those of the district of Nuñoa, the partial pressure of atmospheric oxygen is 40 percent or more below the values at sea level. As noted above, such a deficiency of oxygen produces a multitude of physiological changes in sea-level man, at all ages. We therefore attempted to evaluate the native Indian's responses to altitude at all stages of the life cycle.

Demography. A survey of more than 10 percent of the population revealed an average completed fertility of about 6.7 children for each female. This is quite a high fertility by modern standards, but there was no evidence of voluntary birth control, and cultural practices appeared in many ways designed to provide maximum fertility; under these conditions, 6.7 children is no more than average. This same survey, partially summarized in Table 1, did not show an unusually high rate of miscarriage but did reveal two unusual features. (i) The earliest age at which any woman gave birth to a child was 18 in the low valleys and something over 18 at higher elevations. The average age of first pregnancy was also higher for

Table 1. Statistics on reproduction and viability of offspring for the district of Nuñoa, based on a sample of approximately 14 percent of the population of the district.

Sample	Married women						Sex ratio (males to females) of offspring		Mortality of offspring (%)†	
	Number in sample	Mean age (yr)	Mean age at first pregnancy (yr)	Off-spring (No.)	Mean number of offspring per woman	Mean number of surviving* offspring per woman	At birth	Surviving*	Male	Female
Total sample	136	36.2	19.5+	608	4.5	3.2	124	129	30	33
Sample of postmenopausal individuals	31	45+	20.1	207	6.7	4.4	113	146	27	44

*"Surviving" refers to time of the census. †During the period of growth.

women at the higher altitudes. (ii) The sex ratio was highly unusual in that there was a large number of excess males. Furthermore, there was a higher mortality of females than of males throughout the period of growth. In an associated study of newborns it was found that, for Quechua mothers in Cuzco (altitude, 3300 meters), placenta weights at childbirth were higher and infant birth weights were lower than corresponding weights for comparable mothers near sea level (*4*). Finally, an analysis of the Peruvian census showed that, as in the United States, the mortality of newborn infants is higher at higher elevations; this does not appear to be primarily a socioeconomic correlation. From the results so far obtained, we conclude that fecundity and survival through the neonatal period is probably adversely affected by high altitude, even in the native populations of high-altitude regions. However, it is clear that the Nuñoans can still maintain a continuing population increase. Our data do not provide a basis for deciding whether, at high altitudes, fecundity and survival of offspring through the neonatal periol are greater for natives than they are for immigrant lowlanders (*5*).

Growth. Intensive studies on growth were carried out on over 25 percent of the Nuñoa-district children, from newborn infants to young people up to the age of 21. A number of unusual growth features were apparent shortly after birth. Thus, as shown in Table 2, a slower rate of general body growth than is standard in the United States is apparent from a very early age. In addition, developmental events such as the eruption of deciduous teeth and the occurrence of motor behavior sequences occur late relative to U.S. standards. For example, the mean number of teeth erupted at 18 months was 11.5 for Nuñoa infants as compared with 13 for U.S. infants. The median age at which Nuñoa children briefly sat alone was 7 months, and the median age at which they walked alone was 16.2 months. These data were collected by means of the technique developed by Bayley, who reported that the median ages at which U.S. children sat and walked alone were 5.7 months and 13.2 months, respectively (see *6*).

Some of the growth characteristics in later development are shown in Figs. 2 and 3. In these growth studies it was possible to compare our results with cross-sectional data for groups from lower elevations (Huánuco and Caja-

Table 2. Stature and weights of Nuñoa infants and of infants in the United States.

Age (months)	Stature, males (cm)		Stature, females (cm)		Weight, males (kg)		Weight, females (kg)	
	Nuñoa	U.S.	Nuñoa	U.S.	Nuñoa	U.S.	Nuñoa	U.S.
6	62	66	61	65	6.9	7.6	6.6	7.3
12	71	75	69	74	7.9	10.1	7.3	9.7
24	76	87	75	87	9.9	12.6	9.0	12.3

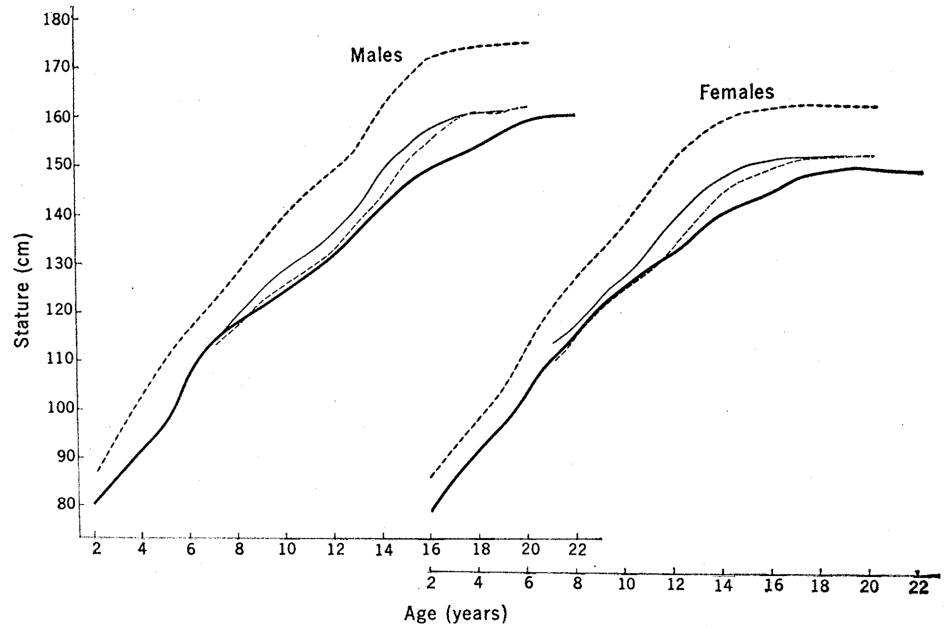


Fig. 2. The growth of Nuñoa children as compared to that of other Peruvian populations and of the U.S. population. (Heavy dashed lines) U.S. population; (light solid lines) Peruvian sea-level population; (light dashed lines) Peruvian moderate-altitude (1990 to 2656 meters) population; (heavy solid lines) Nuñoa population (altitude, 4268 meters).

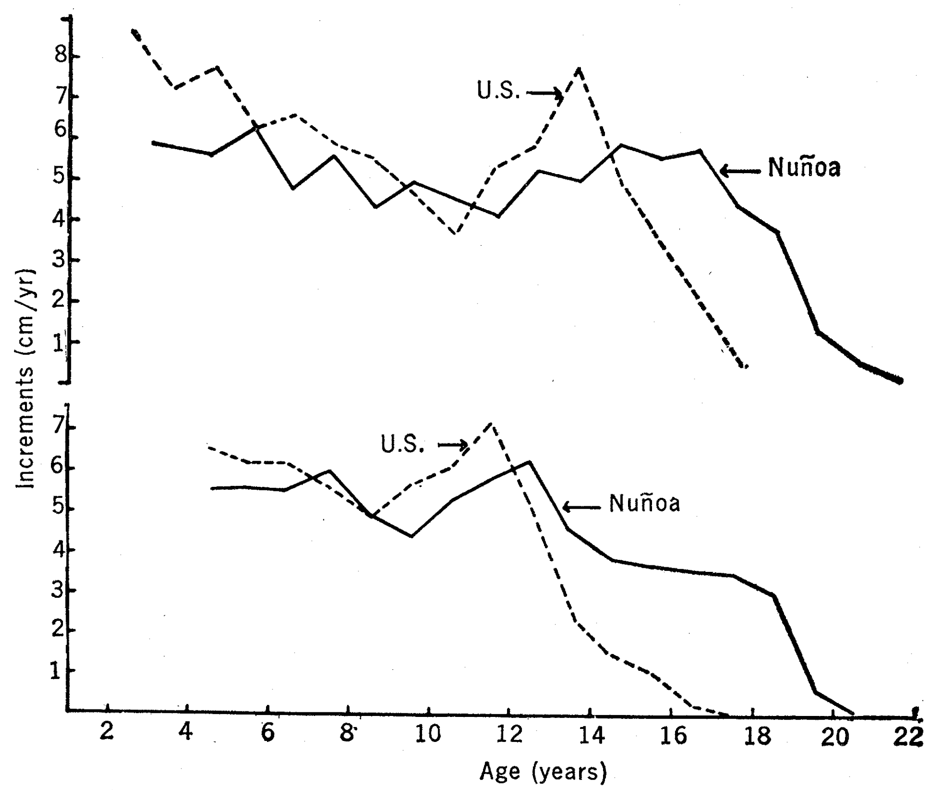


Fig. 3. Rates of general body growth for children in Nuñoa as compared with that for children in the United States. (Top) Males; (bottom) females.

Fig. 4. A Nuñoa native beside his house during a brief snow squall.

marca, 2500 meters; Lima and Ica, 300 meters). We have also collected some semi-longitudinal data in order to evaluate growth rates. These combined data (7) showed, for Nuñoa children, (i) lack of a well-defined adolescent growth spurt for males, and a late and poorly defined spurt for females; (ii) a very long period of general body growth; and (iii) larger chest sizes, in all dimensions and at all ages, than those of children from lower elevations.

In explanation of the unusual growth aspects of the Nuñoa population, at least three hypotheses may be suggested: (i) all Quechua have an unusual growth pattern, genetically determined; (ii) malnutrition and disease are the prime causes; (iii) hypoxia is the major factor. Our present data are not adequate for testing these hypotheses. However, a number of observations suggest that hypoxia is a major factor. As discussed below, we have been unable to find any evidence of widespread malnutrition or of unusual disease patterns. What data are available on the growth of other Quechua show growth patterns different from those found for the Nuñoans (8). Finally, hypoxia has been shown to affect growth in a number of animals other than man (3).

Work physiology. The most striking effect of high altitude (4000 meters) on newcomers, apparent after the first few days of their stay, is a reduced capacity for sustained work. This reduction is best measured through measurement of the individual's maximum oxygen consumption. For young men from a sea-level habitat, the reduction is in the range of 20 to 29 percent; the men who had received physical training generally showed a greater reduction than the untrained (9). Some rise in maximum oxygen consumption occurs during a long stay at high altitudes, but studies extending over periods of as much as a year have failed to show a recovery to even near low-altitude values for adult men (10).

Maximum oxygen consumption for any individual or group is controlled by a large number of factors, among which the level of continuing exercise is of major importance. Among young men of European descent, mean values for maximum oxygen consumption range from below 40 milliliters of oxygen per kilogram of body weight for sedentary groups, through 45 milliliters per kilogram for laborers, up to more than 55 milliliters per kilogram for highly trained runners (11). The high degree of variability in this parameter makes it difficult to determine whether the native of a high-altitude region has a work capacity different from that of an individual from a low-altitude habitat, and makes it even more difficult to determine whether the complex physiological differences between groups from high and low altitudes have resulted in a better adaptation, with respect to work capacity, for the high-altitude Quechua.

In order to help clarify these questions, we determined maximum oxygen consumption for a number of carefully selected samples of contrasting populations; in all cases the method of determination was the same. Some of the results of these studies are presented in Table 3. It should be noted that the individuals referred to as White Peruvian students are so classified on the basis of morphology, and it is quite possible that they contain some admixture of native Quechua genes.

On the basis of results obtained for students alone, one investigator surmised that the differences in maximum oxygen consumption for high-altitude and low-altitude groups might be only a matter of life-long exposure, plus a high state of physical fitness in the highland Quechua (12). In an article based on partial results (13), some of the investigators, including myself, pointed out that trained athletes from lower altitudes could, at high altitudes, achieve the same oxygen consumption per unit of body weight as the Nuñoa native. While the data now available support the idea that physical training and life-long exposure to hypoxia act to increase maximum oxygen consumption, these two factors appear insufficient to explain the total results. The data, instead, suggest that a fairly random sample of Nuñoa males between the ages of 18 and 40 have a vastly greater maximum oxygen consumption than a group of reasonably physically fit researchers from the United States. The oxygen consumption of the Nuñoans also significantly exceeded that of young native students from lower altitudes, and equaled that of a group of highly trained U.S. athletes who had spent a month at high altitude. Furthermore, the heart rate and ventilation rate for the Nuñoans remained low. The Nuñoans do walk more than people from the United States, but nothing in the personal history of the Nuñoa subjects suggested that they had experienced physical training or selection comparable to that involved in becoming a college track athlete. To me, the data suggest that a high-altitude Quechua heritage confers a special capacity for oxygen consumption at 4000 meters. In the absence of more precise data, such a conclusion remains tentative. However, the data can certainly be interpreted as showing that the Nuñoa native in his high-altitude habitat has a maximum oxygen consumption equal to, or above, that of sea-level dwellers in their oxygen-rich environments. This conclusion is in agreement with the results obtained by Peruvian researchers (*2*).

Cold

The microenvironment. By the standards of fuel-using societies, the temperatures in the Nuñoa district are not very low, and we would consider the typical daily weather equivalent to that of a pleasant fall day in the northern United States. However, the lack of any significant source of fuel made us suspect that at least some segments of the population might suffer from significant cold stress. As mentioned above, few trees grow in the district, and those that do are slow-growing. At present, these trees are used primarily as rafters for houses; only an occasional member of the upper class uses wood for cooking. The fuel used almost universally for cooking is dried llama dung or alpaca dung. This dung provides a hot but rapid fire, and is burned in a clay stove, which provides little external heat. Since cooking is done in a building separate from the other living quarters, only the women and children benefit from the fire. Bonfires are lit only on ceremonial occasions; the winter solstice is celebrated by a pre-Hispanic ceremony in which many bonfires are lit all over the district. The use of fires during solstice ceremonies throughout the world is often considered an act of sympathetic magic to recall the sun. For Nuñoans it may also recall the warmth.

The houses of the native pastoralists, with walls of stacked, dry stone and roofs of grass, provide no significant insulation. Measurements made within the dwelling units generally showed the temperature to be within 2° or 3°C of the outdoor temperature. This is in sharp contrast to the situation in the adobe houses used by the upper classes, by some agriculturalists in the Nuñoa district, and by all classes in slightly lower areas of the Altiplano. Adobe houses provide good insulation, and indoor temperatures are frequently 10°C above outdoor temperatures during the cold nights of the dry season.

From this analysis and other observations we concluded that the Nuñoa native depends upon his own calories for heat, and relies, for heat conservation, primarily upon his clothing and upon certain customs, such as spending the early evening in bed and having as many as four or five individuals sleep in the same bed. As shown in Fig. 4, his clothing is layered and bulky, with windproof materials on the outside. Thus, it provides good insulation for his body. However, the Nuñoa native's wardrobe does not include gloves, and the only foot coverings are sandals occasionally worn by men. The insulating effect of native clothing was tested under laboratory-controlled cold conditions. It was found that at 10°C the clothing increased mean body temperature by about 3°C and raised the temperature of hands and feet despite the lack of gloves and shoes.

From the total assessment we concluded that the Nuñoa native probably experiences two types of exposure to cold: (i) total-body cooling during the hours from sunset to dawn and (ii) severe cooling of the extremities, particularly in the daytime during periods of snow and rain. To assess the degree of stress due to cold we took measurements of rectal and skin temperatures of individuals in samples selected by sex, age, and altitude of habitat. These studies indicated that at night the adult women experience very little stress from cold, whereas adult men showed some evidence of such stress. During the day, women, because they are less active than men, may experience slight stress from cold, whereas men do not, except for their extremities. Active children show no evidence of such stress; however, during periods of inactivity, as at night, their skin temperature and rectal temperature are low. Indeed, at these times, all indices show an inverse relationship between age, size, and body temperatures (*14*).

Physiological responses. In order to characterize the Nuñoa native's responses to cold, we used three types of laboratory exposures: (i) total-body cooling at 10°C with nude subjects, for 2 hours; (ii) cooling of the subject's

Table 3. Some data from tests of maximum oxygen consumption (max V_{O_2}) at high and low altitudes for contrasting populations.

Group of subjects	Altitude at which tested (m)	Duration of exposure to high altitude	Subject				Response*					
			Number	Mean age (yr)	Mean height (cm)	Mean weight (kg)	Max V_{O_2} (liter/min)	Aerobic capacity† (ml/kg/min)	Maximum ventilation (liter/min)	Ventilation equivalent‡ (V/V_{O_2}/min)	Maximum heart rate (beat/min)	Oxygen pulse (ml/beat)
Nuñoa Quechua	4000	Life	25	25	160	57	2.77	49.1	75	27.3	171	16.0
U.S. white researchers	300		6	30	183	79	3.92	50.4	131	33.7	185	21.2
U.S. white researchers	4000	4 weeks+	12	27	181	75	2.78	38.1	91	32.9	173	16.6
U.S. white athletes	300		6	20	179	71	4.58	64.2	131	28.8	175	26.5
U.S. white athletes	4000	4 weeks	6	20	179	71	3.14	46.6	105	33.7	172	19.4
Quechua from sea level	100		10	22	160	62	3.01	49.3	108	36.2	187	16.7
Quechua from sea level	4000	4 weeks	10	22	160	62	2.67	44.5	87	33.4	190	14.5
Peruvian students												
Quechua	3830	Life	10	23.8	162	60	2.79	46.8	72	25.8	188	15.1
White	3830	Life	13	23.5	169	61	2.62	42.8	74	28.2	186	14.2

*The measurements were made by means of a bicycle ergometer in 10-minute progressive exhaustion tests. †Aerobic capacity is the maximum oxygen consumption per kilogram of body weight and, as such, is the most significant measure available of the success of the individual's (and, by inference, the group's) biological oxygen transport system. It is also assumed to be one of the best measures available for judging an individual's work capacity relative to his body size. ‡Ventilation equivalent is the ventilation volume per unit oxygen uptake per unit time. The lower the value, the greater the relative efficiency in supplying oxygen.

Table 4. Exchange of body heat as exemplified in heat production and heat loss. The values are averages for two exposures at 10°C, expressed on the basis of body-surface area.

Subjects	Number in sample	Heat production (kcal/m²)			Heat loss* (kcal/m²)		
		1st 60 minutes	2nd 60 minutes	Total time	1st 56 minutes†	2nd 60 minutes	Total time
Whites	19	51.5	62.2	113.7	29.6	11.8	41.4
Nuñoans	26	58.1	65.5	123.6	51.0	12.9	63.9
Lowland Indians	10	54.7	65.5	120.2	30.1	14.7	44.8

*Heat not replaced by metabolic activity. †Because perfect equivalence in body temperature prior to exposure to cold was not achieved, heat loss in the first 4 minutes of exposure has been excluded from this calculation.

hands and feet at 0°C, for 1 hour; (iii) cooling of the feet with cold water. The subjects were Nuñoa males and females, North American white males, and Quechua males from low-altitude habitats.

Some results of the studies of total-body cooling are summarized in Table 4. Since the Nuñoa Indians are smaller than either the coastal Indians or U.S. whites, the data are presented in terms of surface area (*15*). Viewed in this way, the data show that the native Quechua from a high-altitude habitat produced more body heat during the first hour than individuals from low-altitude habitats, but produced amounts similar to those for such individuals during the second hour. By contrast, heat loss was much greater for the Nuñoans than for members of the other groups during the first hour and similar during the second hour. The findings on heat loss are perhaps the more interesting, since they conform with results of two other studies of cooling responses in native Quechua from high-altitude habitats (*16*).

When the source of the greater heat loss was closely examined, it proved to be almost entirely the product of high temperatures of the extremities, and these temperatures, in turn, seem to be produced by a high flow of blood to the extremities during exposure to cold. When a comparison was made, as between Nuñoa males and females, of the temperatures of the extremities, the women were found to have warmer hands and somewhat colder feet. In both sexes the temperatures for hands and feet were significantly above corresponding values for white male subjects. The specific studies of hand and foot cooling made with exposures of types ii and iii shed further light on the subject, showing that the maximum differences between populations occurred with moderate cold exposure; that the high average temperatures of hands and feet were the result of a slow decline in temperature, with less temperature cycling than is found in whites; and that the population differences were established by at least the age of 10 (the youngest group we could test) (*17*).

Since the oxygen exchange between hemoglobin and tissue bears a close positive relationship to temperature (*18*), it is clear that, when the temperature of the peripheral tissues remains high, more oxygen is available to these tissues. Therefore, the high temperatures of the extremities of the Nuñoans at low atmospheric temperatures may be considered not only an adaptation to cold but also a possible adaptation to hypoxia.

Nutrition and Disease

In the complex web of adaptations that are necessary if a peasant society is to survive, adequate responses to nutritional needs and prevalent diseases are always critical. For a people living at high altitude, these responses are important to an interpretation of the population's response to altitude and cold.

Nutrition. The analysis of nutritional problems in the Nuñoa district has proceeded through a number of discrete studies, including a study of dietary balance in individuals, a similar study for households, an analysis of food intake by individuals, and a study of the metabolic cost, to the community, of food production. Of these studies, the first two have been completed, the third is in the analysis stage, and the fourth is in the data-collection stage. The results to date suggest that the Nuñoa population has a very delicate, but adequate, balance between nutritional resources and needs.

The dietary-balance study was carried out with six native adult males, chosen at random. Food requirements were predicted from U.N. Food and Agriculture Organization standards, on the basis of weight and temperature. The food used in the study consisted wholly of native foodstuffs and was prepared by a native cook. The results showed that, for these individuals, protein, caloric, and fluid balance remained good, and indicated that caloric and protein balance was good prior to the time of the study (*19*). The household survey suggested that nutrition for the population as a whole was generally adequate, although the method did not permit conclusions on the adequacy of nutrition for special subgroups, such as children and pregnant women (*20*).

The household survey also suggested that the diet might be somewhat deficient in vitamin A and ascorbic acid. Subsequent, more detailed surveys of individuals now cast doubt on the validity of this conclusion and suggest that, if malnutrition exists, it is probably no more common than in U.S. society. Indeed, in the light of the modern concept of "overnutrition," we might even say that the Nuñoans have a better dietary balance than the U.S. population. As noted above, the balance is delicate, and there must be years and times of the year when certain dietary deficiencies exist. Furthermore, the balance is subtle. To cite an example, the basic foods available are very low in calcium, yet adequate calcium is obtained, primarily by use of burned limestone as a spice in one type of porridge (*21*).

Disease. Our data on infectious disease are particularly inadequate. Health questionnaires are almost useless, since native concepts of health are only partially related to modern medicine. The *indígenas* attribute over 50 percent of all illness and death to *susto*, a word best translated as "fright." As noted above, no regular medical treatment is available, so records are lacking, even for a subsample. In our general survey we encountered the usual variety of infectious diseases and had the impression that respiratory ailments, such as tuberculosis and pneumonia, were common. On the other hand, we did not find evidence of deficiency diseases—not even goiters.

Perhaps the most striking results of the survey were those relating to cardiovascular disease. In the survey, heart murmers were common among children, but no evidence of myocardial infarction or stroke was seen. Casual blood pressures of individuals from age 10 to 70+ were taken. They revealed a complete absence of hypertension, the highest pressure encountered was 150/90 mm-Hg. Other researchers have reported similar results for high-altitude populations, and it has been suggested that hypoxia may directly reduce the incidence of hypertension (*22*). In an attempt to trace the etiology of the low blood pressures, we subdivided our sample into a series of paired groups, first into lower- and higher-altitude groups, next into urban and rural groups, finally into more acculturated and less acculturated groups.

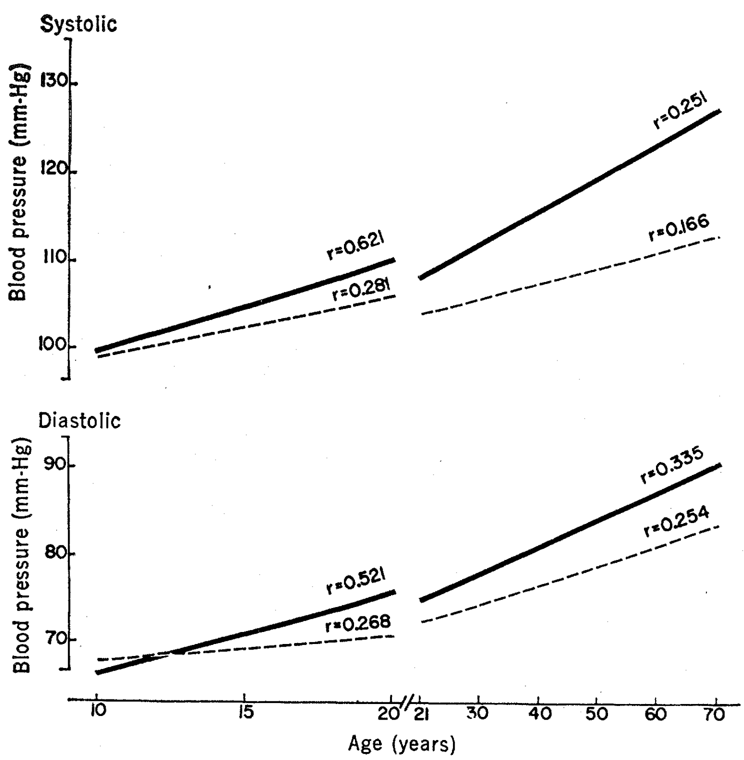
Significant differences in the effect of age on blood pressure appear when the sample is divided on the basis of any of these three criteria. However, it is not possible to assess the extent to which the environmental factors are independently related to blood pressure, since the total sample is too small to provide six independent subsamples large enough to give meaningful analytical results. It is our present belief that acculturation is the most significant of the factors, since altitude, urban residence, and acculturation are interrelated within the Nuñoa district population and the group differences are most striking when acculturation is taken as the criterion of subdivision. Children aged 10 to 20 years were classified as "acculturated" if they were in school, whereas children in the same age bracket who were not in school were classified as "unacculturated." Among adults, evidence of schooling, knowledge of Spanish, and use of modern clothing and specific material items, such as radios, were taken as signs of acculturation.

The results of these comparisons are shown in Figs. 5 and 6. Certainly the regressions cannot be taken as evidence that altitude does not affect blood pressure, since none of the Nuñoa males, even those in the acculturated group, have high blood pressures in old age. However, the analysis does show that, within a native population living at high altitude, something associated with the process of acculturation into general Peruvian society leads to significant increases in systemic blood pressure with age. Similar results have been reported for peasant and "primitive" populations at low altitudes, and some researchers have attributed the increase to psychological stress associated with modern culture (*23*). Such an explanation might apply to the results of our study, but it does not appear safe to conclude that this is the case before carefully examining nutritional and disease correlates. The available nutritional data are being examined for evidence of possible nutritional differences between the groups.

Discussion and Conclusions

From earliest recorded history it has been recognized that men from different populations vary in physical (that is, anatomical) characteristics and in cultures, but it is only recently that the variety of *physiological* differences has been revealed. The physiological differences so far shown are of the same general magnitude as the anatomical variations. That is, the available information suggests a basic commonality with respect to functions such as temperature regulation, energy exchange, and response to disease, but comparison of different populations has revealed a number of specific variations in response to environmental stress.

Probably the most controversial aspect of these new findings concerns the mechanisms underlying the physiological differences. Because of the time and expense involved in studying the problem, population samples have often been small. Thus, with respect to specific findings, such as the high oxygen-consumption capacity reported by some workers for natives living at high altitudes, it has been suggested that biased sampling explains the difference. Other differences have been explained in



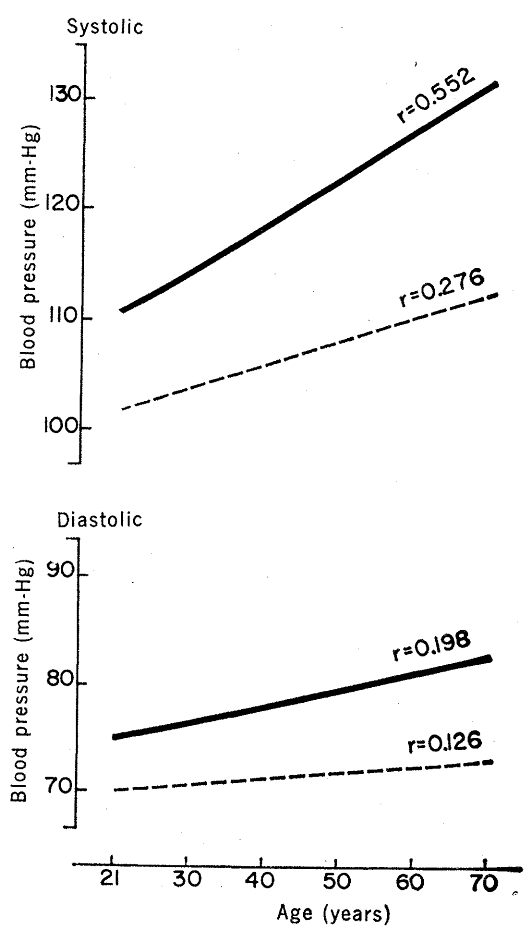


Fig. 5 (above). Changes with age in the blood pressure of male Nuñoa natives, according to level of acculturation. (Solid lines) More acculturated; (dashed lines) less acculturated; *r*, Pearson correlation coefficient. Fig. 6 (right). Changes with age in the blood pressure of female Nuñoa natives, according to level of acculturation. (Solid lines) More acculturated; (dashed lines) less acculturated; *r*, Pearson correlation coefficient.

terms of short-term acclimatization or of variations in diet or in body composition. Of course, genetic differences and long-term or developmental acclimatization have also been suggested, but the short-term processes have been more commonly accepted as explanations because they are based on known mechanisms.

We believe that a more general application of the extensive and intensive methods used in studying the Nuñoa population is a necessary next step in the search for the sources of differences in functional parameters in different populations. Thus, with respect to the Nuñoa population, a study of growth alone would probably have led to the conclusion that the observed differences in growth were the result of malnutrition.

On the other hand, the results of the growth study considered together with results of detailed studies of nutritional and other responses suggest hypoxia as a better explanation. Similar examples could be cited, from other aspects of the program, to show that a set of integrated studies of a single population can provide insights not obtainable with data pertaining to a single aspect of population biology.

In general, the data are still not adequate to treat the third question originally posed, on the sources of adaptation. Indeed we cannot even clearly differentiate genetic factors from long-term and developmental acclimatization. For this purpose one would require comparable data on several populations that vary in genetic structure, in altitude of habitat, and in other aspects of environmental background. Fortunately, collection of such data is contemplated as part of the Human Adaptability Project of the International Biological Programme. The importance of understanding the sources of population differences seems obvious in a world where the geographical and cultural mobility of peoples is greater than it has ever been throughout history.

It seems clear that the native of the high Andes is biologically different from the lowlander, and that some of the differences are the result of adaptation to the environment. How well and by what mechanisms a lowland population could adapt to this high-altitude environment has not yet been adequately explored. Moreover, almost nothing is known about the biological problems faced by the highlander who migrates to the lowlands.

Summary

The high-altitude areas of South America are in many ways favorable for human habitation, and they have supported a large native population for millennia. Despite these facts, immigrant lowland populations have not become predominant in these areas as in other parts of the New World, and lowlanders experience a number of biological difficulties on going to this region.

In order to learn more about the adaptations which enable the native to survive at high altitudes, an intensive study of a native population is being carried out in the district of Nuñoa in the Peruvian Altiplano. In this area hypoxia and cold appear to be the most unusual environmental stresses. Results to date show a high birth rate and a high death rate, the death rate for females, both postnatal and prenatal (as inferred from the sex ratio at birth), being unusually high. Birth weights are low, while placenta weights are high. Postnatal growth is quite slow relative to the rate for other populations throughout the world, and the adolescent growth spurt is less than that for other groups. The maximum oxygen consumption (and thus the capacity for sustained work) of adult males is high despite the reduced atmospheric pressure at high altitude. All lowland groups brought to this altitude showed significant reductions in maximum oxygen consumption. The Nuñoa native's responses to cold exposure also differ from those of the lowlander, apparently because blood flow to his extremities is high during exposure to cold. The disease patterns are not well known; respiratory diseases appear common, whereas there seems to be almost no cardiovascular disease among adults. Systemic blood pressures are very low, particularly those of individuals living in traditional native fashion. Nutrition appears to be good, but analysis of the nutrition studies is continuing.

The results of these studies are interpreted as showing that some aspects of the natives' adaptation to high altitudes require lifelong exposure to the environmental conditions and may be based on a genetic structure different from that of lowlanders.

References and Notes

1. C. Monge, *Acclimatization in the Andes* (Johns Hopkins Press, Baltimore, 1948).
2. *Life at High Altitudes; Proceedings of the Special Session held during the Fifth Meeting of the PAHO Advisory Committee* (Pan American Health Organization, Washington, D.C., 1966); *Arch. Inst. Biol. Andina* (this is a new journal devoted entirely to the subject of acclimatization at high altitude; address, Apartado 5073, Lima, Peru).
3. E. J. Van Liere and J. C. Stickney, *Hypoxia* (Univ. of Chicago Press, Chicago, 1963).
4. J. P. McClung, *Amer. J. Phys. Anthropol.* **27**, 248 (1967).
5. C. Hoff, thesis, Pennsylvania State University (1968).
6. T. S. Baker, A. V. Little, P. T. Baker, "Infant Development at High Altitude," in preparation.
7. P. T. Baker, R. Frisancho, R. B. Thomas, in *Human Adaptability to Environments and Physical Fitness*, M. S. Malhotra, Ed. (Defense Institute of Physiology and Allied Sciences, Madras, India, 1966).
8. R. Frisancho, thesis, Pennsylvania State University (1966).
9. E. R. Buskirk, J. Kollias, R. F. Akers, E. K. Prokop, E. Picon-Reategui, *J. Appl. Physiol.* **23**, 259 (1967).
10. From results of a study of adult men over a 1-year period and inferences from cardiovascular changes found only in the high-altitude newborn, Velasquez concludes that adults from lowland regions can never adapt to high altitudes as well as natives do [T. Velasquez, in *The Physiological Effects of High Altitude*, W. H. Weihe, Ed. (Macmillan, New York, 1964)].
11. K. L. Andersen, in *The Biology of Human Adaptability*, P. T. Baker and J. S. Weiner, Eds. (Clarendon, Oxford, 1966).
12. R. B. Mazess, thesis, University of Wisconsin (1967).
13. J. Kollias, E. R. Buskirk, R. F. Akers, E. K. Prokop, P. T. Baker, E. Picon-Reategui, *J. Appl. Physiol.* **24**, 792 (1968).
14. J. M. Hanna, thesis, University of Arizona (1968); P. T. Baker, in *Human Adaptability and Its Methodology*, H. Yoshimura and J. S. Weiner, Eds. (Japan Society for the Promotion of Sciences, Tokyo, 1966).
15. P. T. Baker, E. R. Buskirk, J. Kollias, R. B. Mazess, *Human Biol.* **39**, 155 (1967).
16. P. T. Baker, in *The Biology of Human Adaptability*, P. T. Baker and J. S. Weiner, Eds. (Clarendon, Oxford, 1966); R. W. Elsner and A. Bolstad, "Thermal and Metabolic Responses to Cold Exposure of Andean Indians at High Altitude," *Ladd Air Force Base Tech. Rep. AALTOR 62-64* (1963).
17. M. A. Little, thesis, Pennsylvania State University (1968).
18. This conclusion is based on the shift in the oxygen disassociation curve produced by lowering blood temperature. A standard graph, such as that presented by Consolazio and his associates [C. F. Consolazio, R. E. Johnson, L. J. Pecora, *Physiological Measurements of Metabolic Functions in Man* (McGraw-Hill, New York, 1963), p. 112] illustrates this effect.
19. E. Picon-Reategui, "Food Requirements of High Altitude Peruvian Natives," unpublished.
20. R. B. Mazess and P. T. Baker, *Amer. J. Clin. Nutr.* **15**, 341 (1964).
21. P. T. Baker and R. B. Mazess, *Science* **142**, 1466 (1963).
22. M. J. Fregly and A. B. Otis, in *The Physiological Effects of High Altitude*, W. H. Weihe, Ed. (Macmillan, New York, 1964).
23. N. A. Scotch, *Amer. J. Public Health* **53**, 1205 (1963).
24. The data presented in this article represent the work of many scientists on the project. I particularly want to cite the contributions of Drs. E. R. Buskirk, J. Kollias, G. DeJong, and G. Escobar (all affiliated with the Pennsylvania State University) and of E. Picon-Reateguie (Universidad de San Marcos), M. Little (Ohio State University), R. Frisancho (University of Michigan), R. Mazess (University of Wisconsin), and J. Hanna (University of Hawaii). I also want to note the invaluable assistance of Mr. Victor Barreda and the officials of the Nuñoa district. The research is continuing as a U.S. project under the International Biological Programme. The primary financial support for the project was provided by the U.S. Army Medical Research and Development Command under contract DA-49-193-MD-2260. Additional support was provided by that Command (contract DA-49-193-MD-2709), by the Public Health Service (grant IROI HD-01756-01), by the National Institutes of Health (grant GM-07325-03), and by the Pennsylvania State University and the Instituto de Biología Andina.