

Introduction

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ABSTRACT A basic premise of studies conducted in the 1950s and 1960s was that humans exhibited a uniform set of biological responses to the high altitude environment. Since then, investigations have been carried out in the North American Rockies, South American Andes, and the Himalayas by researchers from a variety of disciplines—biological anthropology, respiratory physiology, cardiology, hematology, and nutrition. These studies have contributed important insights for understanding the mechanisms involved in adaptation to high altitude and have revealed possible differences in the strategies of adaptation exhibited by the world's various high altitude populations. However, the findings have sometimes been slow to percolate across disciplinary boundaries, given the tradition among the biological sciences to conduct research and present findings in specialized groupings. This symposium breaks this pattern by bringing together from several disciplines investigators who are actively involved in the conduct of high altitude studies. The interaction afforded enables us to realize that understanding the process of human adaptation to high altitude requires a holistic approach whereby the expertise of various scientific disciplines needs to be utilized in a synchronized and integrated manner.

The comparative nature of this symposium is evidenced in two ways: by studies which address the effects of high altitude on different groups residing in the same locale (Leonard and Greksa) and by studies which compare high altitude populations from the various world regions (Moore, Beall, Winslow, and Schoene). In so doing, these studies call attention to the importance of cultural and nutritional factors determining the effects of high altitude exposure and the physiological processes dictating transport of oxygen to the tissues.

Andean populations have been reported to have a slow growth in stature and an accelerated growth in lung volume. More than 20 years ago, we postulated that the slow growth in stature reflected the effect of hypoxia (Frisancho, 1975). However, the work of Leonard, Leatherman, Carey, and Thomas (this issue) demonstrates that the slow growth of Andean residents is related to the limited energy availability characterizing their high altitude environment. Furthermore, Leonard and co-workers show that the distribution of food and nutrients among households is strongly influenced by socioeconomic factors and as such, the pattern of

growth at high altitude may be a function of hypoxia as well as of socioeconomic factors.

The effects of high altitude may be strongly influenced by the phase of life during which they begin. The developmental adaptation paradigm (Frisancho, 1975) implies that the critical functional and morphological traits that enable humans to adjust to high altitude environments need to be acquired during the period of growth and development. As inferred from previous studies (Frisancho and Greksa, 1989; Stinson, 1985), it appears that the enlarged lung and chest size observed in Andean natives is acquired through an accelerated rate of growth. Furthermore, as indicated by Greksa (this issue), the enlarged lung volumes are established very early in life and become accentuated during the developmental period. Indeed, as conclusively shown in dogs (Johnson et al., 1985), growth in a hypoxic environment increases lung volume and alters structure whereas an equivalent length of exposure in adult animals does not. This change in lung structure is reflected in

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an enhancement of pulmonary diffusing capacity of populations living in the Rocky Mountains and the South American Andes (DeGraff et al., 1970; Vargas et al., 1982). In addition, Greksa confirms previous findings which indicated that achieving a normal maximal aerobic capacity is dependent upon being exposed to low-oxygen pressure during growth (Frisancho et al., 1973; Frisancho, 1975). The measurement of maximal aerobic capacity provides an excellent index of functional adaptation because it represents the integrated functioning of all the components of the oxygen transport system, e.g., ventilation, circulation, and tissue metabolism. Since even European children growing up at high altitude show this developmental trait, it does not appear to be unique to Andean native high altitude residents. It remains to be seen the extent to which the same principle of developmental adaptation can be applied to explain the aerobic capacity of the Himalayan high altitude natives.

The effects of high altitude on growth begin in utero, leading to a reduction in infant birth weight but not length of gestation. The studies of Moore (this issue) present evidence that Himalayan, Rocky Mountain, and Andean populations differ in terms of the fetal growth retardation observed. Remarkably, Tibetan birth weights are similar to sea level values, whereas the North and South American samples show the expected reduction in birth weight. Furthermore, comparisons of characteristics of maternal oxygen transport influencing fetal oxygen supply suggest that babies born to the Tibetan pregnant women may benefit from a redistribution of blood flow to favor an increase in uterine perfusion. However, although Andean newborns weigh less than those at sea level, lower birth weights are not necessarily a sign of maladaptation. While low birth weight is correlated with increased infant mortality, Beall (1981) indicates that the birth weight associated with the lowest mortality at high altitude (3,860 m) is 3,462 gm whereas this value at sea level is 3,632 gm. Thus, low birth weights in Andean populations may not adversely influence newborn survival. Different pathways for response to high altitude may be involved in which Himalayans engaged in redistribution of blood flow to preserve fetal growth whereas Andean residents display a reduction of tissue mass as evidenced by lower birth weights.

Various investigators have reported that the hemoglobin concentration among Hima-

layan populations is lower than that of Andean high altitude residents. As shown by the studies of Beall, Brittenham, Macuaga, and Barragan (this issue), the lower hemoglobin levels of Himalayan compared to Andean populations do not appear due to differences in the techniques of data collection. Frisancho (1988) indicated that rural non-mining Quechua populations have hemoglobin levels which were similar to the Himalayan values. However, Beall and colleagues report that rural, non-mining Mestizo Andean residents tend to have higher hemoglobin concentrations than the Himalayan persons studied. Sampling differences may be involved insofar as the Andean studies included both native and Mestizo populations while the Himalayan groups were more homogeneous. In support of a hemoglobin difference between the Himalayan and Andean regions, the report by Winslow, Chapman, and Monge (this issue) shows that for a given hematocrit, erythropoietin concentrations are higher in residents of Chile than in those of the same altitude in Nepal. This suggests that the hypoxic stimulus is greater in the Andes than in the Himalayas or that some other factor, such as red cell lifespan, may differ between the two regions. Related to the possibility that differences in hypoxic stimulus may influence hemoglobin levels were their observations that the Sherpa residents of Nepal with higher hematocrits had less ventilatory responsiveness to hypoxia than did those with lower hematocrits. Another possibility is that for geographical reasons, high altitude exposure for the Himalayans may be more intermittent than for the Andeans. If Himalayan residents do have lower hemoglobin concentrations than Andean residents, an important unanswered question is whether the observed differences have biological meaning.

Previous studies have demonstrated that Andean residents are able to perform maximal exercise at a lower ventilation than are sojourners, suggesting that oxygen diffusion in the lung, cardiac output, or oxygen diffusion at the tissue level may be enhanced. Schoene (this issue) confirms that Andeans are able to preserve their arterial oxygen saturation at maximal exercise despite an apparently low and blunted hypoxic ventilatory response. In this regard, they differ from previous studies of sojourners for whom the ventilatory sensitivity to hypoxia appears to be an important factor for raising ventilation and arterial oxygen saturation. The blunted

hypoxic ventilatory response in native highlanders appears to be acquired and is not limited to a specific population since it occurs also among Europeans with long-term residence in the Rocky Mountains (Byrne-Quinn et al., 1972). Whether or not it is present among Himalayan residents is unknown.

In sum, it appears from this symposium that human adaptation to high altitude can no longer be viewed simply in terms of low oxygen availability but must also incorporate recognition of the factors dictating oxygen transport and tissue metabolism. Furthermore, the responses present in Rocky Mountain, Andean, and Himalayan high altitude residents appear to differ in several potentially important respects. Continuing, collaborative research on the part of physiologists and biological anthropologists such as reported here promises to advance our understanding of the human capacity to adapt to environmental stress.

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