POPULATION STUDIES ON HUMAN
ADAPTATION AND EVOLUTION
IN THE PERUVIAN ANDES

Edited by
Robert B. Eckhardt and Terry W. Melton

Number 14

1992

POPULATION STUDIES ON HUMAN ADAPTATION AND EVOLUTION IN THE PERUVIAN ANDES

Edited by Robert B. Eckhardt
and Terry W. Melton

Department of Anthropology
The Pennsylvania State University

TABLE OF CONTENTS

FOREWORD

The first volume of The Pennsylvania State University Occasional Papers in Anthropology was published to report progress on a long-term study of human adaptation to high altitude. Of particular concern were the biological and behavioral mechanisms which had adapted the Andean populations to their high altitude environment. Previous research primarily by Peruvian scientists had established that the highland Quechua had the ability to function normally in this environment both in terms of mental and physiological parameters. The extent to which a group of lowlanders could achieve a similar response was not known.

It has been established that the debilitating physical symptoms which appear in most people after a rapid ascent to an altitude in the 3000-5000 m range will generally disappear after a few days. This is the consequence of respiratory adaptation and acclimatization. However there are persistent effects which include a reduced maximum oxygen consumption capacity. This restriction reduces both the ability to perform hard work and durability in moderate physical activity. It was generally assumed that this deficiency would disappear within a few weeks as hemoglobin levels rose. However most evidence suggested that a full recovery would take longer.

Our research did not support the idea that a substantial improvement would occur in a few months or even years. However the relatively good performance at altitude of natives who had spent their adult lives near sea level suggested that growth and development at high altitude might improve the oxygen transportation system. Thus the idea of a long-term developmental adaptation which might require birth and growth in reduced oxygen pressure environments was developed. Later research by Frisancho further supported the idea. This concept did not, of course, rule out the possibility that genetic selection might in part account for the high oxygen consumption capacity of the high altitude natives in the Andes.

Among the many physiological characteristics which can potentially enhance oxygen consumption capacity is a large lung volume. A larger size relative to muscle mass could enhance oxygen diffusion to the blood thereby increasing its availability to body cells. Indeed Peruvian highland groups are known to have large forced ventilatory capacities compared to lowlanders. Concomitant with the large lung volumes and ventilation capacities is a large chest relative to body size and some unusual rib cage characteristics including a long sternum and flared lower ribs.

A variety of studies over the part twenty years have sought to answer whether these unusual physiological and morphological characteristics are a consequence of developmental

adaptation to hypoxia or are a consequence of genetic adaptation. There has been evidence that at least to some extent lung function and perhaps chest morphology is altered by spending the growth period at high altitude. However some researchers have found that the unique chest characteristics of the Peruvian highland native are not altered by growth and development.

Eckhardt and his students present additional evidence to support this finding. Furthermore they make a forceful case for accepting that the unusual chest morphology and small body size of the altiplano Quechua and Aymara have a strong genetic base. They suggest that this is primarily the result of natural selection. I, for one, am inclined to agree with their conclusions.

The series of studies reported in this volume demonstrate how time consuming and demanding heritability studies can be but as the results show, barring a major breakthrough through human genome mapping, such studies are critical for understanding how selection shaped our species.

Paul T. Baker
Evan Pugh Professor Emeritus of Anthropology

PREFACE

The body of data on which this monograph is based was collected by the principal investigator and a small group of professional associates during four seasons of fieldwork in Peru. Subsequently, the analyses were all carried out in the material and intellectual milieu provided by a liberal arts college situated within a large public university with a strong research tradition. In the main the analytical work was accomplished by graduate student colleagues working sequentially rather than simultaneously. This made for a relationship between the project director and each successive student that often was close, but also has resulted in repetition of some of the introductory material from one chapter to another, since these originally comprised independent works of scholarship. These publications have been edited once again here, but more to accomplish greater uniformity of style than to effect any significant alterations of substance.

Readers also should be aware that this monograph is addressed to several rather different audiences: to human biologists who are interested in studies of human adaptability, specifically to those concerned primarily with altitude adaptation; to geneticists and other evolutionary biologists who are interested in the study of interactions among inherited and environmental factors in extant populations of vertebrates over periods of time that encompass higher multiples of generations than commonly can be studied in laboratory populations; and to paleoanthropologists and other paleontological specialists who are interested in the development of complex morphological characteristics within and between populations that are known to belong to only a single lineage, but one which has undergone measurable differentiation over a limited span of time.

Because the intended readership is unusually diverse, it is inevitable that many of its members will find certain aspects of the subject matter included here to be unsatisfactory in one way or another. A specialist in high altitude physiology may feel that there is too little material on respiratory function to be of interest, while a specialist on morphology may wonder why lung function was studied at all. The same treatment of a quantitative genetic approach that might seem opaque to a paleoanthropologist almost must of necessity appear elementary to a specialist in evolutionary genetics. Paleontologists accustomed to studying a fossil record that documents apparent morphological stasis for hundreds of thousands of years may be unimpressed by evidence that some morphological attributes characteristic of high altitude populations did not change from one generation to the next when a population long resident in one environment shifted to one that is radically different, while human biologists used to

encountering substantial developmental plasticity will find the same results to be quite unanticipated. For all of these attributes of the monograph that may appear as shortcomings to one specialist or another, and for many more that can and perhaps will be encountered, my suggestion is that each result reported here be considered in context of the objectives and scope of this study. No one could be more aware than I that far more data are needed to address properly some of the topics that could only be touched upon here, and that more sophisticated approaches can and will be developed to extract even more reliable results from additional data that should be added in the future to what we have provided so far.

The work that is offered here, then, is not represented as a final word on the biology of a particular human group; rather, it is intended as a catalyst for further studies into the genetic continuity of past and present human populations.

Robert B.Eckhardt

ACKNOWLEDGEMENTS

Any large-scale and long-enduring scientific investigation is, of necessity, a cooperative endeavor. This project is no exception. Its progress to this point has involved the contributions of many people who, because they are not represented here as authors of the chapters included in this monograph, consequently merit some explicit recognition at the outset.

As elaborated in greater detail in the Introduction, the initial conception of the project arose in the course of discussions with Paul T. Baker, who edited the monograph, titled High Altitude Adaptation in a Peruvian Community, which was the first volume in this series of Occasional Papers in Anthropology published by The Pennsylvania State University. Subsequently both Paul Baker and his wife Thelma provided significant help in various ways: advice based on their own prior field experience, introductions to Peruvian colleagues, loans of a microfilm camera and other items of equipment, and so on. It is doubtful that the project would have begun as swiftly and smoothly as it did without their aid.

The Bakers also were instrumental in recommending James S. Dutt, then a faculty member at James Madison University, as a member of the first year's field team. In the course of his earlier graduate work at Penn State, Jim had spent an extensive amount of time in the Andean highlands. It was suggested that he could thus supply the experience that the principal investigator initially lacked. In practice these expectations were fully realized, with Jim proving to be reliable in emergencies, indefatigable in data collection, and amiable even under the most challenging of circumstances. He contributed heavily to the success of the project in its most critical beginning phase.

In Peru our progress was facilitated by official contacts and networks of friendship already established by the Bakers during the course of their own fieldwork. Foremost among the Peruvians with whom I was placed in contact and in whose debt I stand are Dr. M. Tulio Velásquez and Melquiades Huayna Flores. During the periods of our research in Peru (1978, 1980, 1981, and 1986), Dr. Velásquez held various posts, including Director of the *Instituto de Biología Andina* and Dean of the Medical School of the University of San Marcos. In these official capacities and as a friend he eased our way through daunting logistical and bureaucratic problems in a foreign country whose culture was significantly different from our own. Because of his critically important help at more points than I can report or even recall, it became possible for us to accomplish large amounts of work over very limited periods of time.

Among all of the varied and valuable services that Dr. Velásquez performed on our behalf, beyond doubt his single most important act was to suggest that we recruit Melquiades

Huayna Flores as a member of our research team. Prior to our project, Melqui had accumulated several decades of experience in high altitude research conducted under laboratory and field conditions. As a result he had become not only a Jack of all trades, but master of many: laboratory technician, mechanic, guide, linguist, and all-around ambassador of goodwill. Melqui participated fully in all four field seasons of data collection, and his contributions throughout the project were pervasive and invaluable. Melqui, my wife Carey and I formed the constant core of the team that collected data over the period that lasted from 1978 through 1986.

The network of others who facilitated the project extends outward in a number of directions. Two archeologists in the Anthropology Department at Penn State, William T. Sanders and David Webster, helped me to develop the necessary background in Peruvian prehistory. My former Penn State colleague Gabriel Escobar, now retired as a university professor but still conducting research in Peru, provided much valuable background information on that country's history and culture. He also provided considerable technical assistance in translating questionnaires into Spanish and Quechua. Still further, Gabriel put us into contact with his family in Peru; subsequently, many of his relatives provided help of various sorts, but none more than Felix and Nati Blanco. Close to us in age and outlook, they came quickly and easily to share our enthusiasm for the research from the moment of our initial contact during the first field season. In all of the ensuing years their home in Lima became our informal center for planning and communications. There, hospitality and friendship provided a supportive setting for the wise counsel that they often offered us.

In the highlands our work was facilitated by Dr. Julio Bustinza, Rector of the *Universidad Nacional Tecnica del Altiplano (UNTA)* in Puno. Dr. Bustinza suggested several populations in the Lake Titicaca region that might be willing to cooperate with our research initiative. After we had selected the village of Camacani, which bordered UNTA's agricultural experiment station, he also generously provided us with living quarters and rooms for use as laboratories.

For reasons discussed in greater detail in Chapter 1 of this volume, we enjoyed relations with members of the Camacani and other study populations in the Lake Titicaca region that were not only cordial but collegial in a quite literal sense: many of the people in the populations that we studied qualified as colleagues in the spirit that they strove to understand the questions that we were investigating and encouraged others to work with us as well, thus furthering the project to a measurable degree. This level of cooperation was so common that it would be invidious to single out only a few people for special recognition. Consequently, our

gratitude is extended to all of the members of the communities of Camacani, Coata, and Huata who did so much to further our research.

For the later phase of the investigation carried out within the lowland city of Tacna in 1981, special thanks are due to Padre Luis Mellado, Director of the parish school of San Martin de Porres. Padre Mellado provided space for our work, encouraged the students and their parents to cooperate with us, and allowed us access to school records so that we could verify the dates and places of birth of the students who were included in our sample of offspring born at low altitude to parents of high latitude ancestry. Recognition is due as well for the school teachers who adjusted their curricular plans around our research schedule, and to the parents who not only gave us permission to take batteries of anthropometric measurements on their children, but also allowed us into their homes so that they, too, could be measured. Finally, in this regard, we thank the students themselves for their overall high levels of cooperation, good spirits, and lively interest. It was our impression that although the investigators and students learned different things about each other, the exchange of knowledge was as equitable as it was enjoyable for all concerned.

Finally, we would like to express our thanks for the financial and material resources that have been invested in this project. Initial funding was provided by Biological Research Support Grant number RR0707082-11 administered by The Pennsylvania State University. Part of the subsequent data analysis was supported by 1 R01 HL 25400-01 awarded to the principal investigator by the National Heart, Lung, and Blood Institute of the National Institutes of Health. Later phases of related field research were funded through BRSG Grant Number 2S07 RR0707082-21 and by two grants from the Harry Frank Guggenheim Foundation. Small amounts of supplementary funding were provided by The Pennsylvania State University from the Fund for Academic Excellence and the Liberal Arts Central Fund for Research.

Two corporations deserve special attention for aid which they provided not to the project itself, but through it to Peruvian people and institutions. These instances of corporate support provide some particularly clear perspectives on the power of private industry to reduce the gaps between individual human aspirations and the societal constraints on resources that exist in many Third World countries.

The first case leading to corporate assistance arose when, at the end of the 1978 field season I was approached by Camacani community delegates with the question of whether we could help them acquire an electric generator to illuminate the school at night for adult education classes. Few adults were as yet able to read, although many wished to attain the levels of literacy being reached by their children. However, the community's school was too

distant from the University's agricultural experiment station to be served by its small and sporadically operative electric power plant. I could promise only to try to help, without making any guarantees. Some of the early attempts that I made in this regard were time-consuming but unsuccessful. However, just before our return to the Peruvian highlands in 1980, I contacted Dan Conlon, President of Instruments for Industry and Research. I knew that it was the policy of his company to accept orders for research equipment from any source, but to place any profits from defense-related purchases into a fund for distribution to various charities. In response to my query he agreed that helping to further adult literacy in Camacani was a worthwhile charitable act, so contributed the funds to purchase an electric generator. We took this with us and, after substantial difficulties clearing Peruvian customs, presented it to the community in 1980.

The second case ensued during the following year, 1981. In the course of preliminary communications with Dr. Velásquez to arrange the forthcoming field season, I learned that several programmable calculators purchased by the *Instituto de Biologiá Andina* with the aid of a small external grant had disappeared in shipping. I immediately contacted Texas Instruments Corporation and explained the situation. Without cavil or charge they immediately shipped six replacements, which we were able to present to our surprised and gratified Peruvian collaborators.

These two examples of corporate responses to our requests for aid on behalf of others affected by our project illustrate what a market-based economic system can yield best: rapid and uncomplicated solutions to individual problems. The larger lesson delivered--and received--in Peru was that U.S. technology could have a human face. When political and economic stability eventually return to Peru and to other developing nations, there will be numerous other opportunities to deliver this message, with potential advantages to all who are involved in such transactions.

It would be unthinkable to close without recognizing the pervasive and continuous support provided by many members of my family. As noted elsewhere, my wife Carey was a full participant throughout all of the field phases of the project, during which she provided much in the way of organization, creativity, and persistence. I know of no one who is so capable of maintaining or generating goodwill under what commonly were the most trying of circumstances. Her involvement in the research program has been integral and essential. Our children--David, Jonathan, Amy, and Jennifer--spent the 1980 field season with us as we commuted daily between our base in Camacani and the sites of our research in Coata and Huata. As a result they shared weeks comprising six or seven days of work for twelve to fourteen hours

per day, with three to four hours of each span spent huddled in the back of an open truck before sunrise and after sundown. In compensation they got mountain sickness, typhoid, an astonishing diet, complete freedom from showers for several months, a bathroom without running water but with running mice and chickens, and a variety of other experiences the value of which they are coming to appreciate only years later. During the three other field seasons that our children remained at home, they were in the care of my mother, Mary Eckhardt. Not surprisingly, all involved in the arrangement have agreed that her care was preferable to ours. Really, no one could have expected to have done a better job than she, given the value of experience: our children were the third generation of the family that she has helped raise, and she is now shaping the lives and characters of yet a fourth.

The chapters that are included here all bear appropriate credit for their respective authorships. Special thanks are due, however, to Terry W. Melton. After completing the most recent of the studies for this project, she went on to do an enormous amount more work to prepare the text, figures, tables and references for publication. These efforts represent the investment of months of work, without which the delay in publication of this monograph inevitably would have been much longer.

Robert B. Eckhardt

CHAPTER 1

GENETIC AND ENVIRONMENTAL FACTORS INFLUENCING HUMAN VARIATION AT
HIGH ALTITUDE: BACKGROUND, PLANNING, AND EXECUTION OF THE PROJECT

Robert B. Eckhardt

INTRODUCTION

For one of his books on popular science, the polymath J.B. S. Haldane chose the title
Everything Has a History. The spirit symbolized by that phrase pervades this monograph:
the subject dealt with here is rooted in at least ten millennia of prehistory, a period that
encompasses the minimum span of human existence in the Andean highlands. Human
occupation of the Andean high plateau, or *altiplano* , is an impressive phenomenon because of
the scale that it has attained against a challenging background: a population that began from
a few wandering hunters and gatherers has grown into a population well over ten million
people living at altitudes ranging from about 2500 meters (about 1.5 miles) to over 5000 meters
(about 3 miles), in environments that are characterized not only by rugged terrain, poor soils,
and wide temperature ranges, but also by an atmosphere with a partial pressure of oxygen that
is only about 60% to 70% of that found at sea level.

Just as human habitation of the Andean highlands has a history (and an even longer
prehistory), so does the study of adaptation to life in the *altiplano.* Scientific research into
the biological effects of existence on the high plateau has developed through a sequence of
steps over a period encompassing several generations of investigators; and they, in turn, built
upon foundations of knowledge that had been established centuries before as Spanish scholars
recorded their impressions both of the long-antecedent indigenous cultures and of their own
responses to environments that the newcomers found unfamiliar and physiologically stressful.

BACKGROUND

A Previous Phase of Research

It is not my intention to review here the entirety of the voluminous antecedent
literature on the mechanisms of human adaptation to high altitude ecosystems; several of the
chapters included within this monograph, most notably those by Ahn (whose doctoral
dissertation was completed in 1990) and even more recently Melton (whose M.S. thesis was
completed in 1991) accomplish that task so satisfactorily as to render redundant any further
elaboration by me along such lines. Nevertheless, it would be less than candid to neglect

recognition of one of the more recent, clearly identifiable steps in high altitude research, particularly because that antecedent work led to my own involvement in the study of adaptation and evolution in the Andean region of South America. The earlier investigations referred to here were those headed by Paul T. Baker and documented, among other places, in the very same publication series as this current volume. The monograph edited by Baker appeared in December, 1968, as Number 1 of the *Occasional Papers in Anthropology* published by The Department of Anthropology at The Pennsylvania State University.

In his introductory chapter to that monograph, Baker (1968) noted that he and his collaborators from The Pennsylvania State University and the *Instituto de Biologiá Andina* at the University of San Marcos in Lima, Peru, had decided to explore the biological and cultural characteristics of an ecologically stable high altitude Andean population living in traditional fashion in the district of Nuñoa, Peru. The general research problem that motivated their project was subdivided into three specific questions: (1) What are the unique environmental stresses to which the population has adapted; (2) How has the population adapted culturally and biologically to these stresses; and (3) How did the adaptive structures become established in the population?

The results generated in response to these questions were quite extensive.   The first *Occasional Papers* monograph edited by Baker comprised 563 pages of reports and appendices authored by at least eight investigators who discoursed on topics as diverse as socio-political organization, demography, reproduction, exercise performance, cold stress, nutritional response, and even the effect of coca chewing on metabolic balance. These findings can be seen as having formed a broad foundation for subsequent research. As a result of these efforts at least one local area in the South American high altitude ecosystem, that of Nuñoa, had been documented in detail; the social organization and demography of its Quechua inhabitants were described; their occupational categories and subsistence bases were known; within this context their health status and growth patterns had been summarized; and the impacts of cold, physical exercise, and hypoxic stress had been investigated on small samples of subjects.

Despite the abundance of data gathered and analyzed by Baker and his research team, however, some central questions remained unanswered when their *Occasional Papers* monograph was published. In the section titled <u>Discussion and Conclusions,</u> Baker noted that "...in relation to specific findings, such as the high oxygen consumption capacity reported by some for high altitude natives, it has been suggested that biased sampling explains the difference. Other differences have been explained on the basis of short-term acclimatization or dietary and body compositional variation. Of course, genetic differences, as well as long-term

or developmental acclimatization, have also been suggested; but the short-term processes have been more commonly accepted explanations because they are based on known mechanisms.... In general, the data are still not adequate for differentiating genetic factors from long-term and developmental acclimatization. To do so would require comparable data on populations which vary in genetic structure, in altitude, and in a variety of environmental backgrounds.... In the high Andes it seems clear that the population is biologically different from lowlanders, and [that] some of the differences are adaptive to the environment. How well and by what mechanisms a lowland population could adapt to this environment is still inadequately explored. Equally, the biological problems faced by the downward migrant remain almost unknown." The volume's Summary continued the same theme, concluding that "The results are interpreted as showing that some aspects of native adaptation take lifelong exposure to the environmental conditions and may be based on a genetic structure which varies from that of lowlanders."

Whether there were identifiable genetic contributions to norms and variations in the distinguishing physical and physiological characteristics of high altitude Andean people such as those resident in Nuñoa and elsewhere remained unresolved. The results that had been obtained by Baker and his associates in response to such queries were suggestive but not definitive. In hindsight it is possible to observe that the data that they collected could not have provided explicit answers to these questions, without detracting from either the heuristic value of their questions or the empirical significance of their data. Their efforts did, however, suffice to establish a plausible basis for pursuing the line of inquiry that had been opened. The findings summarized by Baker (1968) made it clear that high altitude Andean natives were distinguishable morphologically from their lowland counterparts, with thoracic measurements varying about means that were higher, and statures varying about means that were lower, than those encountered in sea level populations. Measures of lung function such as forced vital capacity ((FVC) and forced expiratory volume (FEV) were shown to be correlated positively with these structural features of the thorax, findings that were consistent with a functional explanation for the larger thoracic dimensions in a hypoxic environment. Furthermore, the populations that manifested these features were still living in the rugged, cold, hypoxic environments that had been occupied continuously by their predecessors for at least 10,000 years or some 500 human generations; in other species, populations that had been exposed to less pervasive stresses for shorter periods of time had undergone evolutionary change in one or another of genetic, physiological, and morphological characteristics. Against this background,

the expectation that there might have been genetic contributions to human high altitude adaptation was reasonable. But a direct test of such a hypothesis had not yet been made.

New Approaches to Old Questions

Quite simply, if genetic questions were to be answered, genetic data must be gathered. I was encouraged by Paul Baker to begin collecting such data in 1977. It should be stressed that from the outset the research program that developed under my direction was designed to have a different direction and a tighter focus than the previous high altitude research conducted by researchers based at The Pennsylvania State University. As noted above, their earlier work had identified the various cultural, social, and biological mechanisms that functioned in extant Andean populations. Our new initiative was concerned more with assessing the long-term results of the natural experiment in human evolution that had been going on for ten or more millennia as populations of *Homo sapiens* had expanded into the rugged, cold, oxygen deficient *altiplano* of South America. Various strategies could have been employed in the pursuit of this objective. The one that we chose was quite straightforward: application of some standard techniques of quantitative genetics to infer whether any of the variations in thoracic structure seen in high altitude Andean populations were influenced by genetic as well as environmental factors in their development. The details of this approach are set forth in several of the chapters included in this volume so need not be presented separately here.

Our group's investigation had its own logical foundation, though one that was rather different from that of previous investigators in this domain of research. The central focus of my research long has been the application of explicit genetic models to the analysis of skeletal traits that are used in the reconstruction of long-term human evolution (see Eckhardt 1985, 1987, for specific applications, and Eckhardt 1989 for a review of the subject). These approaches have been developed to provide more objective and testable methodologies to supplement or supplant the traditional, more subjective, reconstructions of human phylogeny that are based directly on fossilized skeletal remains recovered from earlier geological strata. The larger objective of which these approaches form a part is unification of human biology into a single field with a common underlying logical structure. This unification will mark notable progress from the present status of the field, which is characterized by a sharp division between studies of present populations of living humans on the one hand, and past populations represented by fossil hominid remains on the other.

Problems in the Interpretation of Long-Term Human Evolution

Although fossil remains comprise some of our most direct evidence for the study of past human evolution, their interpretation is subject to certain intrinsic limitations. Because samples of fossil skeletal material from any site often are small and fragmentary, it is difficult for investigators to assess accurately the extent of within-population variation or the factors that contribute to it. This problem is further exacerbated by the fact that human skeletal remains recovered from the geological strata deposited hundreds of thousands or millions of years ago often present character complexes that have no exact modern counterparts; as a result, the relative influences of genetic and environmental factors on morphology cannot be investigated directly, and thus permit the unconscious or covert assumption that the observed morphological features represent the direct, uncomplicated expression of underlying genotypes. All of these problems are complicated still further by the difficulties that exist in establishing the chronometric ages of the specimens. Human fossil remains recovered from geological strata that were deposited hundreds of thousands or millions of years ago are not always associated with materials that make it possible to assign dates to them at all; and even when radiometric or other dating techniques can be employed, the estimates of antiquity obtained often have intrinsic error terms on the order of tens or hundreds of thousands of years. An important consequence of this uncertainty in the chronometric ages of fossil remains is that often it is difficult to know whether the populations represented by different fossils were contemporaneous or instead were separated by some large but indefinite periods of time.

The fossil evidence for past human evolution embodies major uncertainties such as these, as well as numerous other problems that are not mentioned here. Paradoxically, in practice paleoanthropology, the branch of human biology that deals with this body of evidence and its interpretation, has come to be characterized by confident assertions about many aspects of hominid phylogeny. Certain fossils are ruled out of the ancestry of subsequent human populations in the same geographic area because it is said that linking the earlier and later groups in an ancestral-descendant relationship would require impossibly rapid rates of evolution in the known skeletal features. As one example, Western European neanderthal populations commonly are said to have been replaced by anatomically modern *Homo sapiens* invaders, even though the fossil evidence is far from compelling in its support of such an interpretation. This and other examples of postulated speciation and replacement by rapid genetic and morphological restructuring of populations often are held to reflect a normative pattern in the fossil record, while gradual phyletic changes in the allelic composition and developmental expression of a population's gene pool are discounted as infrequent and

unimportant. On a larger scale, it even has been maintained that macroevolutionary changes of the sort preserved in the fossil record cannot be explained in terms of the microevolutionary processes that are known to underlie genetic change in extant populations.

The Present as a Key to the Past

Assertions of the sort enumerated above can rarely, if ever, be resolved by direct studies of the fossil evidence itself because of the intrinsic limitations outlined above. However, the millennia-long occupation of the Andean highlands has presented human biologists with a situation in which related hypotheses that are relevant to the interpretation of long-term human evolution can be tested. Human populations native to the *altiplano* must be descended from ancestors who migrated from the lowlands at some point in the past, regardless of which among the several alternative routes proves to be correct. Members of present highland populations are distinguished anatomically and physiologically from lowland populations to whom they are nevertheless connected by gene flow, implying that complete genetic isolation is not necessary for the development of a measurable degree of morphological differentiation. Moreover, the characteristic biological features of present Andean populations have arisen over a period of ten to twenty thousand years, during which timespan no human species other than anatomically modern *Homo sapiens* has existed. Thus extant Andean human populations present us with a case in which there has been measurable morphological change, certainly without speciation, over a period of time that can be estimated with far greater precision than is scarcely ever possible in the hominid fossil record (Eckhardt 1985).

PLANNING AND EXECUTION

From Theory to Practice: How the Project Developed

From the preceding brief background sketch it should be evident that a major objective of this project was to gather and analyze data in a framework that would make it possible to unite the study of present and past populations. Most directly, it was intended to estimate the extent to which genetic as well as environmental factors were contributing to the observed phenotypic variation in the characters selected for study. If the existence of identifiable genetic contributions to variation could be established, it was further intended to explore the possibility that these genetic contributions had been shaped by forces of evolution that had operated through the course of preceding generations. In a broad sense, therefore, the plan was to use the present as a model for testing propositions about the past; to join the modern genetic

and phylogenetic perspectives. It might be noted in passing that these aspirations have been realized to a surprising extent.

If the research outlined above began with a clear conception of what needed to be done, it also was undertaken with an equally clear idea of what could not be accomplished. From the very beginning of the project there were severe limitations on financial resources. Several of the most prominent funding agencies that were approached for large grants at the outset made it clear that in their view high altitude research already had been supported generously for a considerable period of time and if the major questions had not yet been solved, then additional large-scale funding might not be expected to change that situation. From the resultant constraint, of course, others followed. Chiefly due to financial limitations, there were consequent strictures on the time that could be devoted to the study, the numbers of people who could be involved, the types of instrumentation that could be employed, the kinds of information that could be collected, and the pace at which the data could be analyzed. Fortunately, the financial limitations to work were relative rather than absolute. Thus, although funding was modest and its continuity was always in question, we were able to maintain operations through support from a series of smaller grants from several sources, chiefly the National Institutes of Health and the Harry Frank Guggenheim Foundation.

While the financial constraints were unwelcome, not all of their side effects were deleterious. Some of the consequences were even distinctly positive. For one thing, the small study teams that we fielded were neither forbidding, nor were they markedly intrusive into the routine activities of the communities with which we worked. As a result, Peruvian highland communities and individuals accepted us readily. This, in turn, made our efforts at data collection highly productive per unit time invested. The same financial limits also made it impossible for us to deviate from our original objective of gathering primarily anthropometric data on large numbers of families; we simply did not have resources that would allow us to be distracted into other, probably more subsidiary, avenues of inquiry. Thus, unlike some projects that were roughly contemporaneous with this one (see, for example, Schull and Rothhammer, 1990), we did not investigate the influences of trace metals at high altitude (Schull et al., 1990) or the relationship between hearing and hypoxia (Bailey and Weidman, 1990); given the seemingly tenuous relationship, *a priori*, of such investigations to the most central questions about long-term effects of altitude adaptation, as well as their largely indeterminate results *a posteriori*, neither our priorities nor our results can be seriously faulted.

Overall, as a result of interrelated factors of constraint and strategy, concentration on the central quantitative genetic focus of our investigations was rewarded with high sample

sizes and resultant low standard errors for heritability estimates. With the same data we were able to carry out related studies on growth and development at high and low altitude; some of the results from the growth studies provided additional avenues of inference about the relative influences of genetic and environmental factors on thoracic form and body size.

The fact that data collection was episodic, compressed into about two months during each year of the project, rather than continuous, made it possible to alter some aspects of experimental design in light of preliminary analyses. Thus along the way some modifications were introduced, largely to answer questions that arose after data collection had begun. One example of this sort, in which results obtained during the 1978 field season helped to determine what we did during the 1980 field season, is discussed later in this chapter.

Population Samples

During the course of this investigation, the members of the various study populations were informed of and involved in the research to an unusually high degree. This was done in part, of course, to meet the formal requirements that are prescribed by U.S. governmental guidelines for the protection of human subjects. However, we routinely endeavored to do even more than was mandated by the formal rules, in order to ensure that the project would have as much value as possible for the adults and children toward whom our scientific attention was being directed. Our efforts in this regard were amply rewarded from the beginning of the first period of data collection in 1978, when circumstances in the field dictated that we would have to work with an Aymara population rather than the Quechua population that we had planned for. The subsequent high level of cooperation by the Camacani villagers with our data collection efforts came as a surprise to some of our colleagues, because the Aymara had long been stigmatized among anthropologists as unresponsive, truculent and even hostile to outsiders (La Barre, 1948). Reconciliation between the traditional negative stereotype and our own positive experience can is explicable in terms of Schull's (1990) similar findings: "...rapport with the Aymará is not easily established, but can be won if they are candidly apprised of what their participation in a study entails, and perceive some benefit to themselves."

Camacani

The Camacani Aymara community is located along the shores of Lake Titicaca, a short distance outside the city of Puno. In this highland community where we began our study in 1978, contact was initiated through Dr. Bustinza, Rector of the *Universidad Nacional Técnica del Altiplano*, which maintains an agricultural experiment station in the area. Through him we held preliminary discussions with members of the village council and the school council. We

then followed their joint recommendation that the project be described in a public meeting with the community. Our presentation took place in the school courtyard with a major portion of the populace--many hundreds of people--in attendance. There were numerous questions, but no objections, and high levels of interest and enthusiasm were expressed publicly as well as, later, privately.

The remaining step in approval was not only formal, but symbolic in several respects. The next day, our research group and the members of the village council were summoned by the blowing of a trumpet at dawn to a small summit at the edge of the village. There, Jim, Melqui, Carey and I stood in a circle with the council members as they contemplated the possibilities of cooperation with us. Our project was first considered by village council members in a context that was formally public but effectively private as far as we outsiders were concerned, since the open discussion took place in the Aymara language which none of us lowlanders understood. Questions then were directed to us in Spanish. These having been answered to the satisfaction of the various representatives, we proceeded to sign a formal convention prepared by village scribes: we would provide some needed financial support for the school, and village adults and children would be encouraged to cooperate with us on a voluntary basis.

Only afterward did we come to realize that the formal pact preparing the way for cooperation between relatively isolated Andean villagers and foreign scientists equipped with unaccustomed levels of technology--what we had thought to be the centerpiece of the morning's activities--was only a small and predictable part of our impact on the traditional local lifestyle. After all, outsiders were uncommon but not unknown and, finally, tools are tools no matter what their evident level of complexity. Far more unusual, although it had not occasioned comment to us by the members of the council (whether from politeness or shock, we never learned), was the act of Carey joining the otherwise all-male circle of discussants. It was a natural enough behavior pattern for her, since after all she had been a full participant in the project from the first and held a doctorate of her own (though in Comparative Literature rather than in some scientific field). But after the council reached an accord and the circle broke up, the women who had been sitting in groups around the periphery, biding their time spinning and knitting, crowded around her with numerous variations of the same basic question: how did you manage that? Her answer was that she was a *doctora*, a holder of an advanced university degree. This news was met with knowing sighs and nodding heads; it is probable that many seeds of academic ambition among young women of the *altiplano* began to germinate that day.

Huata and Coata

When this study began, the only large body of data on the physical characteristics of

Andean highlanders was that which had been assembled by Baker and his colleagues. Therefore, when we began our initial analyses of anthropometric data, it was logical to compare our findings from Camacani with those from Nuñoa. There were similarities, of course, particularly in thoracic dimensions. But we also found some striking differences (Eckhardt and Dutt 1979; Eckhardt and Kramer 1980): plainly, Aymara men living in Camacani were significantly taller and heavier than Quechua men living in Nuñoa. While the difference was clear, its immediate cause was not. Although the two populations resided at very nearly the same altitude, they differed both in ancestry (to whatever degree that some biological differentiation is reflected in Quechua vs. Aymara ethnicity and language) and environment (Nuñoa being situated in a more rugged, inland montane district characterized by greater fluctuations of temperature and more limited nutritional resources, while Camacani is located immediately adjacent to the shore of Lake Titicaca, which exerts a moderating influence on climate and occasions a greater availability of protein from fishing and dairying).

We realized that it would be possible to resolve this problem of multiple alternative explanations for the same phenomenon by using the 1980 field season to structure controlled ethnic and environmental comparisons. This was accomplished by collecting the same set of anthropometric measurements on a Quechua sample resident in a Titicaca lakeshore environment. These data were gathered in two adjacent areas, Huata and Coata, located on a peninsula along the northwest shore of the lake intermediate between Camacani to the south and Nuñoa inland and in to the north. The data acquired for comparative purposes consisted of anthropometric variables comprising the International Biological Programme's full list, which would permit 38 univariate comparisons as well as several alternative multivariate approaches.

Tacna

By the second year of the project, preliminary analyses of the family data on anthropometric measurements were yielding results that indicated that a moderate fraction of variation in the thoracic complex was attributable to genetic factors (Kramer, 1980 and this volume; Eckhardt, Kramer and Dutt, 1981). Furthermore, the patterns among the heritability estimates for the anthropometric traits were compatible with the idea that selection could have operated to increase thoracic volume in the high altitude Camacani Aymara population- -and presumably elsewhere through the Andean highlands, though in a formal sense, heritability estimates are population-specific. These findings had an important bearing on the long-standing question of whether there were detectable genetic influences on the characteristic body proportions of Andean highlanders. It was our feeling, however, that it would be highly

desirable to have some independent confirmation of our results.

We sought such supporting evidence from a growth study that targeted a specific population segment that had been brought into existence by major demographic shifts within the Andean region. Because of traditionally high birth rates, in combination with declining death rates and limited economic development in the Peruvian highlands, there had been persistent migration to lowland areas. Many of Peru's coastal towns and cities offered greater promise for work, subsistence and housing. Tacna, a city in southern Peru, located in a province of the same name and adjacent to the Chilean border, was a common destination for many migrants from Camacani and surrounding regions of the Andean highlands.

In the city of Tacna we planned to work with families that consisted of parents who themselves had migrated from the highlands but had given birth to children in the region at about sea level. The children would therefore be of high altitude ancestry, but would exhibit phenotypes that had developed through the expression of genes in a lowland environment. Tacna is an ecological setting free from the hypoxia of altitude, but also characterized by other differences from the highlands as well: foremost among these are a more moderate climate and better access to food and medical care. In this setting, it would be possible, once again, to partition out or separate the influences of ancestry and environment: in this case of high altitude ancestry from high altitude environment, since the former (to whatever extent, if any, it was differentiated) would be present while the latter would not.

The specific setting for our research in Tacna was the Catholic parochial school of San Martin de Porres, which was headed by Padre Luis Mellado. Padre Mellado understood and cooperated outstandingly with our plan, and also encouraged the school's teachers and pupils to help us as well. In addition to having a progressive leader, San Martin de Porres had a very large enrollment of over a thousand students, ranging in level from the equivalent of kindergarten through evening adult education classes.

As is usual in field situations, not all went according to plan. For example, we had intended to progress through the school class by class, collecting anthropometric and demographic data only on those pupils who were identified by their teachers or themselves as fitting the model prescribed by our research plan: offspring of high altitude ancestry who had been born and raised only at low altitude. In practice the teachers preferred to send us entire classes and to let us work out with the students who might fit our research design and be inclined to participate in the study. In actuality, once the work started, almost none of the students opted to be left out. Furthermore, the disposition of our time and space were such that it was more efficient to measure everyone first, then to fill out the questionnaires that elicited

the information on family size, composition, ages of members, and places of birth (which subsequently were confirmed against school records). These factors combined to produce a study that was superior in practice than in plan, for several reasons. First, the anthropometric data were collected in a manner that prevented the investigators from knowing until afterward either the subject's ancestry or the length of time lived in the low-altitude environment. Second, data were collected on subjects who had lived at low altitude for differing periods of time; that is, some of the schoolchildren had been born at high altitude and had migrated to Tacna with their parents. These subjects could act as controls from which it could be learned whether the age and duration of exposure to a high altitude in themselves produced detectable effects. Again, the unexpected had occurred and could be capitalized upon to produce results that were slightly different in form and markedly better in quality than had been projected.

It was our original intention to have a low altitude group of low altitude ancestry as a control group. In practice this logically-appealing dimension of the study proved impossible to carry out. Extensive admixture has occurred in coastal regions over the last several centuries, so that all or most lowland Peruvian populations in the Tacna region are complex mixtures of South American Amerindians, Europeans, and Africans. Additionally, any low altitude group could contain genes from high altitude populations, since these regions are by no means isolated from each other. Many complex, interesting, and important studies of differential migration and gene flow remain to be worked out in this region. The identification and study of a suitable lowland control group remains as one objective for future studies. Even in its absence, the results obtained represent advances in our state of knowledge about the biology of Andean populations.

Data Collection and Management

Unless one has been involved with, and even more to the point, in charge of, a project of the sort undertaken here, it is difficult to grasp the nature and scope of the logistical problems that arise. As noted previously, budgets were a constant preoccupation for the Principal Investigator, particularly since funding was secured just one year at a time from a variety of sources. Simultaneously, data collection took place on a relatively ambitious scale, with the simultaneous or sequential involvement of ten investigators and the recruitment of well over 1500 participants. For each of these subjects there was a minimum of two data forms, one for the basic set of 20 anthropometric measurements, and another for basic demographic information including age, sex, place of birth, residence history, family members, and so on. In many cases there were additional data forms eliciting information on reproductive history and health status, the full list of anthropometric measurements specified by the International Biological

Programme, and measurements of long function. Handling all of the paperwork was itself a substantial task. From near the beginning of the project we recognized the value of having the different forms color-coded for ready recognition, particularly when numerous subjects were awaiting study (as commonly was the case; in contrast to reports from some field research projects, our operations drew a constant, heavy flow of interested subjects). On return from the field, computer coding, verification and data processing took substantial amounts of time.

In a period when scientific investigators have an increasingly wide variety of reasonably priced, highly portable battery-powered personal computers to choose from, the management of data, from collection in the field to analysis in the laboratory, would not seem overly burdensome. When this project was initiated, however, such a stage was still in the future. To begin with our data sheets were typed on stencils for a mimeograph machine, with estimated quantities of needed copies printed in Lima at the *Instituto de Biologiá Andina* and trucked with us into the field. If needed, new forms or supplements to existing forms had to be typed onto new stencils. This was difficult to accomplish without an electric typewriter, which we had. But the only source of electricity was a kerosene-powered generator that had to be started by vigorous, prolonged hand cranking. Then the new stencil master had to be driven into Puno, paper and a mimeograph machine located and scheduled, and a time arranged for pickup of the completed forms. Needless to say, after the first time, modifications were thought through with considerable care.

With infrequent exceptions, all anthropometric measurements were made by one team member and dictated to another team member serving as a recorder who entered the data onto a pre-coded computer form. This procedure both speeded the work and helped to catch some types of errors that can arise from misreading numerical scales on measuring instruments. Questionnaires were filled out by one investigator. The language usually used was Spanish, but sometimes a community delegate was needed to translate between Spanish and Aymara or Spanish and Quechua. Under such situations the investigator must be alert to the possibility of an additional level of inaccuracy affecting the information being gathered; spot repetition of certain questions after a time lag can help to guard against some of the potential problems.

All paper forms had numbered blanks for later entry of data into machine-readable format, in what was then a two-step process that now seems unbelievably inefficient and error-prone, necessitating repeated verification. There is no doubt that collecting and processing the same volume of data today would consume much less time, and perhaps could be accomplished entirely in electronic form.

One cautionary note, however, should be sounded at this point: there is something to be

said for the relative permanence represented by the data sheets themselves, and for the inherent redundancy that will accrue once the data that they hold have been encoded electronically. Investigations of the sort described here commonly are undertaken in economically less-developed countries, where the conditions of existence are marginal to desperate, and the cost of a personal computer can easily represent the equivalent of five to ten years of earnings. To guard against the inevitable and understandable temptations, constant vigilance must be exercised. Most experienced fieldworkers have heard stories of a whole season's data being lost or stolen near the end of the study or on the journey home. Some of these accounts may be apocryphal, but all too many are true.

Despite exercising great caution ourselves, but for chance we might have had a similar tale to tell (rather than data to analyze) from the 1980 field season. Our entire field crew drove each day from our base at Camacani to the region of Huata and Coata in an old open-backed pickup truck. All of the accumulated data were carried with us so that we could verify data sheets against subjects to avoid duplication in measurement, as well as check which school or community members remained to be studied. During one trip to the work area we stopped at a pharmacy to pick up medicine for a sick child in the community. As a result of an unclear understanding regarding who was to stay with the vehicle, no one did; when we returned only minutes later, it was noticed that a leather backpack containing a tape recorder, some tools, a field diary, and a bit more gear was missing--but, fortunately, not the worn cardboard box containing hundreds of data sheets immediately next to the pack. From that point onward we have tried to always maintain backup copies of all data, and to hand-carry one while leaving another elsewhere in reserve. Newer technologies employing scanning devices could perhaps be employed to produce reserve copies of data on disks or other electronic media. However they are managed, vigilance and redundancy are essential concomitants of careful data collection.

The critical steps from raw data collected in the field to the results brought together here for the first time were taken originally by students working toward masters or doctoral degrees in genetics and anthropology. Thus, although the chapters appear to represent products (that is, analyses of particular data sets) they really are part of larger processes (the attainment of practical experience needed to function as scientific investigators). In a culture increasingly fixated on the idea that there are quick and easy solutions to complex problems, graduate study and research are among the few areas in which a functioning apprenticeship system still operates. The true products of this system are not independent research reports but independent scholars. Judged by this standard, among others, the project reported on here has already made some notable contributions.

CHAPTER 2

HERITABILITY ESTIMATES OF THORACIC SKELETAL DIMENSIONS
FOR A HIGH-ALTITUDE PERUVIAN POPULATION

Andrew Alan Kramer

ABSTRACT

High-altitude human Andean populations have distinctive morphological and physiological features which distinguish them from their sea level counterparts. Of these features, one of the most striking is a chest that is large relative to the short stature which is exhibited by high-altitude natives. The question arises as to whether this adaptation is a developmental acclimatization repeated anew each generation, a pattern of growth processes controlled by factors which have been incorporated into the gene pool by selection, or a combination of the two influences. Although several previous studies have attempted to resolve the issue, none have had sufficient or appropriate data to distinguish among the above hypotheses. For quantitative traits such as measurements of chest size and shape, selection cannot produce evolutionary change unless heritable variation is present. It is the objective of this thesis, therefore, to establish whether any heritable variation exists in the measurements which describe chest morphology in Andean populations.

In the research reported here, measurements of chest size and shape were taken on high-altitude Aymara Indians native to the village of Camacani, Peru, at an altitude of 3900 meters. Heritability estimates were calculated for these measurements based on midparent-offspring regression, mother-offspring regression, father-offspring regression, and sib intraclass correlation. For the majority of the traits the heritability estimates were low, thus indicating a substantial amount of environmental influence on the variation in chest morphology.

Several of the traits (sternal length, two anterior-posterior chest diameters, and one measure of chest circumference) that contribute to the characteristic form of the high-altitude Andean thorax had moderate heritability estimates. These traits also showed evidence of substantial maternal effects. These findings establish that there is an appreciable heritable component in the thoracic variation present in the high-altitude Aymara population studied.

INTRODUCTION

Stress of High Altitude

Many low-altitude natives traveling to high altitude experience unpleasant physiological and psychological reactions. Immediately noticeable is a shortness of breath, accompanied by respiratory distress and hyperventilation. Other changes include a rapid pulse rate, interrupted sleep, and headaches intensified by activity. Severe physical and mental fatigue often result (Frisancho 1975, Heath and Williams 1977).

The etiology of these symptoms is due to the environmental conditions existing at high altitude (defined here as 3000 m or more above sea level). Among the environmental factors encountered at high altitude are reduced air temperature, increased solar radiation, rough terrain, and a limited nutritional base (Clegg et al. 1970, Heath and Williams 1977). However, by far the most stressful condition for low-altitude migrants is the reduced partial pressure of oxygen (PO_2) in the ambient air. The atmospheric pressure at sea level is 760 mm Hg, but at 3000 m this declines to 520 mm Hg. This in turn reduces the amount of oxygen in the inspired air, causing an oxygen deficiency in the blood and in the tissues which is referred to as hypoxia.

Most migrants from low altitude to high altitude eventually become acclimatized and the symptoms associated with hypoxia recede. However, no matter how long a low-altitude migrant lives at high altitude, his adaptation never seems to be as complete as that of a native born and raised in a high-altitude environment (Hurtado 1932a, 1932b, 1971). These long-term adaptations affect the high-altitude native both physiologically and morphologically, although it is important to note that not all high-altitude populations show the same form of biological adaptation (Clegg et al. 1970). The scope of this thesis is restricted to Andean natives living in Peru. As such, any statements or conclusions made are necessarily limited to the population studied.

Physiological and Morphological Changes

As mentioned above, hypoxia causes a deficiency of oxygen in the blood and to the tissues. Thus some changes must occur which maintain oxygenation of the tissues as high as possible. There are two basic physiological processes in high-altitude natives that operate in this direction. The first takes place along the PO_2 gradient from the inspired air to the tissues, known as the oxygen cascade (Figure 1). There is a diminution in the magnitude of the oxygen cascade for high-altitude natives, compensating for the initial low value (Hurtado 1971, Heath and Williams 1977). Accompanying this is a shift of the oxygen-hemoglobin

dissociation curve to the right, thus permitting increased diffusion and utilization of oxygen in cellular and metabolic activities (Hurtado 1971).

Andean populations also exhibit morphological adaptations which distinguish them from sea level populations. These have been described in detail elsewhere (Hurtado 1932a, Frisancho 1969, Hurtado 1971, Beall et al. 1977, Heath and Williams 1977) and will be summarized here.
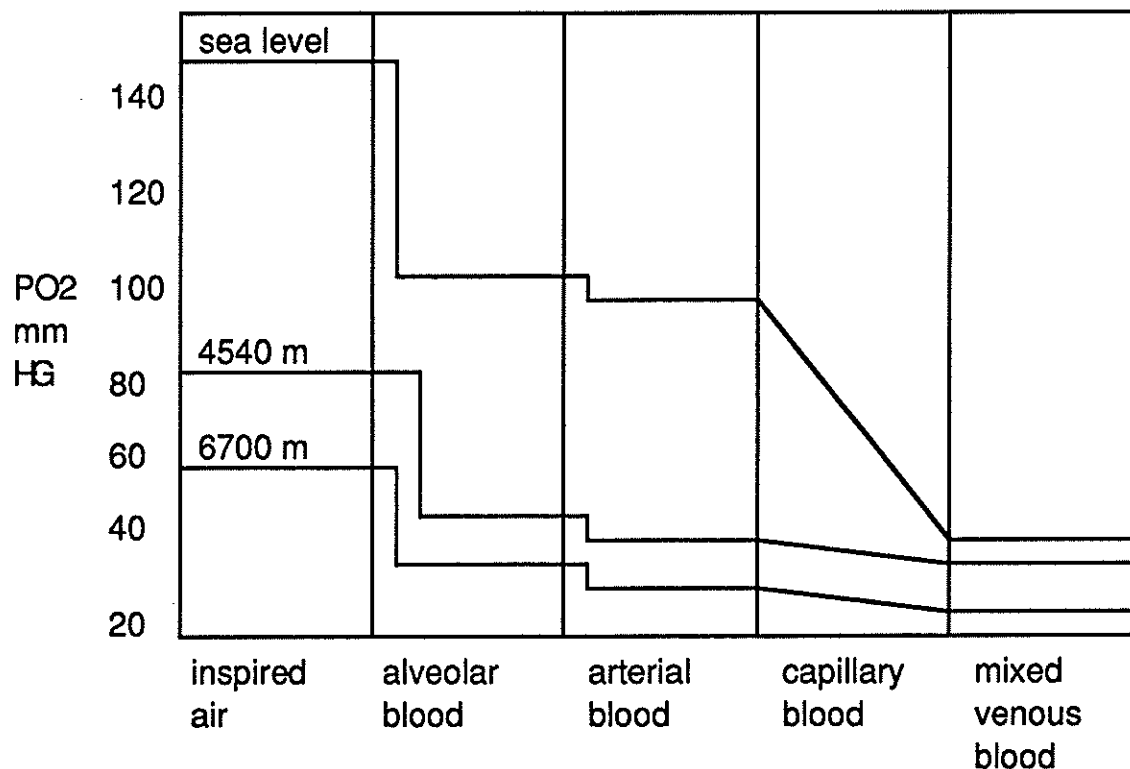
Figure 1. Oxygen Cascade

The Andean native undergoes a slow and prolonged growth period, which results in delayed maturation (Frisancho 1969, Clegg et al. 1970, Hoff 1974, Frisancho et al. 1975). Stature and weight are reduced (Hurtado 1932a, Frisancho 1969, Beall et al. 1977, Heath and Williams 1977) as compared to sea level populations. Yet chest size is increased (Hurtado 1932a, Frisancho 1969, Beall et al. 1977, Mueller et al. 1978b). This increase in chest size is further accentuated when various thoracic dimensions are plotted against stature instead of age (Beall et al. 1977). Thus Andean natives show a disproportionately larger chest size relative to sea level populations. The shape of the chest is often described as "barrel-shaped," but this

metaphor is not totally accurate. It is definitely prominent, but the larger size is due mainly to an increased anterior-posterior depth and cranio-caudal length rather than the symmetrically swelling cylindrical shape which might be inferred from the above term. Along with the allometric growth of dimensions relative to stature, there is an increase in forced vital capacity (Hurtado 1932a, Frisancho 1969).

The morphological features just described are postulated to aid in the decreased rate of decline along the oxygen cascade at high altitude. The larger chest size is associated with larger lung volume. This increase in lung volumes is postulated to permit a larger contact surface between alveolar air and circulating blood in the lung capillaries. Blood flow through the lungs is favored, and the residual volume of air is also increased (Hurtado 1932a, 1971; Heath and Williams 1977). Thus Andean natives can be considered to show adaptive changes which are responsive to an hypoxic environment. This adaptation is not perfect, however. Andean populations are prone to many kinds of illness. These include a higher incidence of heart defects, peptic ulcers, and liver disease (Hurtado 1971), as well as a very common occurrence of juvenile pneumonia (Baker 1978).

Objective

As can be seen, the adaptations to high altitude exhibited by Andean natives are pervasive and complicated. This thesis focuses on one specific point: assessment of the amount of genetic variation that exists in the chest traits that are hypothesized to be part of the adaptive complex.

REVIEW OF PREVIOUS STUDIES

The nature of the forces which shape the characteristic chest morphology seen in Andean populations has been in dispute. One view holds that all differences between lowlanders and native highlanders are due to development of individuals in response to an extreme environment characterized by hypoxia as well as cold and aridity. The other suggests that exposure to such an extreme environment for several millennia could have led to some inherited component in the differentiation of high-altitude Andean populations. At the present time the issue remains unresolved, making it valuable to review some of the previous studies.

Studies Suggesting a Developmental Causation

There have been numerous studies that postulate a developmental causation of the unusual Andean thorax. Among the leading proponents of this position have been Frisancho (1969, 1975) and Frisancho et al. (1975). In one study, Frisancho et al. (1975) compared highland and lowland populations with the same ethnic background (Quechua), resident at those altitudes more than one generation. The highland population generally had larger maximum chest circumferences than the lowland population. Since the two populations showed similarity in their ABO and Rh blood group systems, however, Frisancho and co-workers (1975) concluded that the two populations have similar genetic composition, and that:

> ...the observed growth differences are probably not due to genetic differences
> shown by blood type dissimilarity. In view of these genetic similarities,
> the greater maximum chest circumference of the highland subjects is probably
> of environmental origin...(Frisancho et al. 1975).

However, assuming genetic similarity for all traits on the basis of two loci may not be warranted. Although the two blood group loci show similar frequencies in the two populations, other loci (for example those which might influence skeletal growth and maturation) could be under quite different and possibly stronger selection in one of the populations, producing a genotypically based phenotypic difference in chest morphology between the populations. This possible difference in selection pressures is very important. As has been demonstrated many times under laboratory conditions, once a population that has been exposed to strong selective pressures is relieved of those pressures, the phenotypic response is usually in the direction opposite to that of selection (Falconer 1960). If the hypoxia at high altitude does indeed constitute a strong selective pressure, it is not unreasonable to expect a reversal of selective response in the lowland population. This suggestion is buttressed by the fact that the lowland population studied by Frisancho did not consist of the first-generational offspring of high-altitude natives; thus *at least* one generation of reverse selection could have taken place. Finally, there is also the possibility of genotype-environment interaction taking place.

Another study that advocated environmental causation of a distinguishing feature of high-altitude populations was that of Lahiri and co-workers (1976). The characteristic on which their research focused was the blunted or diminished response to hypoxia usually shown by people native to high-altitude regions. Their purpose was to ascertain whether this response was induced directly by exposure to an hypoxic environment, or whether the blunted

response was attributable to genetic factors present only in high-altitude natives. Their subjects included natives from Tacna (low altitude), Puno (high altitude), and migrants to those cities from regions of contrasting altitudes. On examination for the presence or absence of hyperventilation under simulated hypoxic conditions, young migrants (less than 12 years old) from high to low altitudes showed a normal ventilatory response, but recent migrants (over 15 years old) showed a diminished ventilatory response. Adult migrants at sea level for a long time showed a normal response to acute hypoxia. Of great importance, most (though not even all) of the offspring of lowlanders born and bred at high altitude showed a diminished ventilatory response and increased lung volumes. From these findings the authors postulated that the blunted response to hypoxia is only indirectly related to chest morphology, but is likely to be part of the same complex of adaptations to hypoxic stress.

In their analysis, Lahiri et al. neglect several important factors: 1) none of the migrants from low to high altitudes showed a diminished response to hypoxia, 2) the natives residing in Tacna were generally Mestizos while those living in Puno were of Indian ancestry, hence the populations being compared were of different genetic backgrounds, 3) the sample sizes were disturbingly small; the researchers measured only 58 high-altitude natives 13-20 years old (three per sex per year), and only 40 adult high-altitude natives.

Another paper questioned a possible genetic influence on the grounds that it would have been difficult for Andeans to develop adaptive genes for living at high altitudes because they have not been present there for a long enough period of time (Cruz-Coke 1978). However, recent archaeological studies date habitation in the Andean highlands to at least 11,000 years (MacNeish et al. 1970, Lynch and Kennedy 1970, MacNeish 1971). This represents about 550 generations, clearly enough time for selection to have occurred. Furthermore, the mortality component of Crow's index of selection intensity was shown to be much higher than the fertility component for a high-altitude Quechua population (Garruto and Hoff 1976).

Studies Suggesting a Genetic Causation

Not all hypotheses formed have discounted heredity as being influential. Hurtado (1932a, 1932b, 1971) noticed that acclimatization of a migrant from low to high altitude never is as complete as the adaptation of an Andean born and raised at high altitude. Of particular interest is the appearance since early childhood of "a prominent and large chest as proportionally compared with the rest of the body dimensions" (Hurtado 1932a). Hurtado (1971) goes on to say, though without direct proof, that the Andean native is not only under the

influence of adaptive processes throughout his lifetime, but also under genetic influences that have taken place over many generations.

In a study comparing males in lowland and highland populations, results were found that were in direct contradiction to those reported by Frisancho (Hoff 1974). Five chest measurements were compared between the two populations, and except for chest depth in adolescents, no other chest measurement showed any statistically significant deviation in adolescents or adults. In this study, the lowland natives examined were first-generation offspring of migrants from high altitude, or individuals born at high altitude but resident at low altitudes from an early age. Hoff (1974) states that "there is good evidence to support the thesis that the development of thoracic size and pulmonary function are under strong genetic influence -- as a result of natural selection."

A later study by Beall et al. (1977) compared populations from low altitude (Tambo I), high altitude (Nuñoa), and a group consisting of first-generational offspring born at low altitude to high-altitude parents (Tambo II). Four traits were studied: stature, weight, anterior-posterior (A-P) diameter of the chest, and transverse diameter of the chest. These workers reported that the Tambo II population was intermediate between the Tambo I (taller) and Nuñoa (shorter) populations when stature was plotted against age. This relationship also held when the two chest dimensions were plotted versus age. But when they were plotted with relation to stature, Nuñoa exceeded Tambo II, which in turn surpassed Tambo I for transverse diameters and similarly, Nuñoa residents exceeded those in Tambo I and II for A-P diameters. The authors stated their belief that chest development in the high-altitude Quechua population is not under the same controls as height and weight. Two mechanisms were thought to exist; one independent of hypoxia (chest size), and one influenced by hypoxia (height and weight); it was suggested that the former might be at least in part under genetic control. However, the results of this study must be taken as suggestive rather than conclusive, since in many instances the sizes of the age-sex groups were quite small (less than 8), and in some cases no clear relationship can be discerned.

Recently a large-scale research program was undertaken in Chile to investigate influences on thoracic morphology (Mueller et al. 1978a, 1978b, 1978c). Three groups were studied: Spanish (low altitude, at sea level), Mestizo (low, middle, and high altitudes, equivalent to sea level, 3000 m and 4000 m, respectively), and Aymara (mainly high altitude, again 4000 m). Measurements were taken for various anthropometric characteristics, as well as for lung function. Analyses of multiple regression, principal components, and canonical correlations were done for altitude and a factor called ethnicity. Many results were ambiguous.

In one paper the authors claimed a genetic influence (Mueller et al. 1978a), yet in another they stated an environmental influence (Mueller et al. 1978b). Much of the ambiguity can be attributed to poor experimental design. There were several major problems:

1. Ethnicity was treated as an ordinal measurement, although Mestizos could range anywhere from 1% to 99% Aymara. In fact, it is highly probable that the component of Aymara ancestry increases with altitude, thus confounding the two major influences the study was supposed to distinguish between.

2. Nonsignificant differences were suggested. For example, the A-P diameters of the thorax for different altitude groups were claimed to be different, yet differences between the groups were within one standard error of each other.

3. Inferences from statistical methods were of questionable validity. Regression coefficients were claimed to be significant when the R^2 values were 0.03 - 0.10, and linear regression clearly was not appropriate. The significance of certain variables was claimed on their beta coefficients, while their R^2 values (the appropriate measure of significance) indicated the opposite.

Conclusions Drawn from Previous Studies

As suggested by the brief review of previous work, the nature and balance between proximate influences on chest morphology remain unresolved. This finding underscores the importance of having an experimental design that is adequate to answer the question posed. If anything be drawn from the previous experiments, it is the complexity of causation that may be involved. Perhaps both environmental and genetic influences are involved; since the traits in question are quantitative this is not an unreasonable hypothesis. An environmental influence should exist, as lowland migrants to high altitude do experience acclimatization, even if it is not as complete as in high-altitude natives. But the possibility also exists of genome differences resulting from selection.

MATERIALS AND METHODS

Estimating Heritability

The heritability estimate $\hat{h}^2$ is a genetic statistic commonly used in breeding programs. Its usual function is to aid in assessing the amount of change in a quantitative character that can

be expected using a specific selection intensity. Heritability (h^2) is the population parameter that $\hat{h}^2$ estimates. It can be defined in two ways (Figure 2).

Heritability in the broad sense is the proportion of phenotypic variance in a trait that is due to the genotypic variance. The phenotypic variance is made up of two components, the genotypic variance and the environmental variance. These in turn can be subdivided into more restricted components. The genotypic variance is comprised of three parts: variance due to the additive effects of the genes (breeding values), variance due to interaction of alleles at a single locus (dominance deviations), and variance caused by interaction between loci (epistatic interaction). The environmental variance is made up of two parts: environmental variance within a family, and environmental covariance (between families).

$$h^2_{broad} = V_g/V_p \qquad h^2_{narrow} = V_a/V_p$$
$$V_g = V_a + V_d + V_i$$
$$V_E = V_{Ew} + V_{Ec}$$
$$V_p = V_g + V_E$$

V_g=genotypic variance,V_a=additive variance,V_d=variance due to dominance deviations, V_i=variance due to epistatic interactions,V_E=environmental variance, V_{Ew}=variance within families, V_{Ec}=environmental covariance,V_p=phenotypic variance

Figure 2. Heritability Formulas

It should be mentioned that heritability is population specific (Falconer 1960, Mueller 1975). All components of the genotypic variance are partly based on the underlying gene frequencies of the population. Because gene frequencies can change temporally and differ from one population to another, and environments can vary among populations and through time, the heritability estimate is population – and time – specific.

Heritability in the broad sense is a purely descriptive parameter. Heritability in the narrow sense is the more useful measure for animal and plant breeders. It is the proportion of the phenotypic variance that is made up of the variance due to the additive effects of genes. The reason for h^2_{narrow} being studied instead of h^2_{broad} is simple; only a sample of half of the genes from each parental genotype get passed from one generation to the next; consequently the variance due to dominance deviation or epistatic interaction is not inherited.

The heritability estimate is based on the resemblance between different groups of relatives. Table 1 gives the methods most commonly used. As can be seen, either regressions or intraclass correlations are calculated depending on the relationship examined. Also shown are the proportions of the variance components that the covariance measures.

Table 1. Methods of Estimating h^2

Relationship	Proportion of the Variances that the Covariance Measures $\dfrac{V_i}{}$						Regression b; Intraclass Correlation t $\hat{h}^2$
	V_a	V_d	V_{aa}	V_{ad}	V_{dd}	V_{Ec}	
Single Parent-Offspring	1/2	—	1/4	—	—	—	2b
Midparent-Offspring	1/2	—	1/4	—	—	—	b*
Sib Analysis	1/2	1/4	1/4	1/8	1/16	1	2t
Half-Sib Analysis	1/4	—	1/16	—	—	—	4t

*since V_p is also halved

Each method has its advantages and limitations. Due to the paucity of half sibs in human populations, that method of analysis is usually not practical. In sib analysis, $\hat{h}^2$ contains a term due to dominance deviations. The environmental covariance term (Ec) is also larger in estimates based on sib analysis than those based on parent-offspring pairs. Since the environmental sources of covariance are lower in father-offspring pairs than mother-offspring pairs, it is sometimes the preferred method (Falconer 1972). When there is assortative mating present, the regression of offspring on midparent is recommended (Falconer 1972). Depending on the human population being studied then, either the father-offspring regression or the midparent-offspring regression is the most valid method to use.

There are two factors to keep in mind when estimating heritability. One is the minimization of Ec which is accomplished by choosing the correct method (see above). The other concerns the standard error.

Because $\hat{h}^2$ is a statistic, it has a sampling error which in part determines the validity of the term. For example if a heritability is obtained of 0.40 ± 0.25, then a range of 0.15 to 0.65 is obtained. Clearly the $\hat{h}^2$ tells us very little in that instance. But if the standard error is reduced to 0.15, $\hat{h}^2 \pm$ 1 S.E. is 0.25 to 0.55. This is a bit more revealing. To get a standard error of 0.15, 200 parent-offspring pairs or 150 midparent-offspring pairs are needed (Falconer 1963). Any study done should be structured to attain at least this level of accuracy.

With these strictures in mind, part of an ongoing study has been conducted to estimate heritabilities for various thoracic traits in an Andean population. The next section will describe the population studied and the measurements taken and the following section will present the methods employed to obtain heritability estimates.

Procedures of the Experiment

Camacani is a small village in the Department of Puno, Peru. It lies at about 3900 m, and has approximately 2100 inhabitants, chiefly of Aymara descent. A field expedition in the summer of 1978, led by Dr. Robert B. Eckhardt, studied people in this village as part of a continuing program to assess the relative contribution of altitude and genetics to the thoracic morphology characteristic of native high altitude Andean populations. The natives were primarily engaged in agriculture as an occupation, and had relatively little formal education.

Children were administered a questionnaire, the major purpose of which was to document age, sex, place of birth, and place of residence. Adults completed a more lengthy form, including a health survey. The adult questionnaire not only asked age, sex, place of birth, and place of residence, but also had a list of nine socioeconomic questions included to assess the extent of environmental homogeneity along with marital history. This was followed by a list of offspring. The final segment of the adult form was a general health survey. It was designed to assess the overall health of the respondent, with particular focus on cardiac and respiratory ailments.

A set of 20 anthropometric measurements was taken on both children and adults (Figure 3). These included four International Biological Programme (IBP) measurements (Weiner and Lourie 1969) for overall body size, five IBP measurements for body composition, and six IBP measurements for chest size and shape. Also included in the study were six non-IBP measurements designed to give a better resolution of thoracic morphology. Preliminary results verified the importance of such measurements (Eckhardt and Kramer 1980).

Figure 3. Anthropometric Measurements Taken

IBP Overall Body Size Weight Stature Sitting Height Bi-Iliac Diameter	IBP Body Composition Upper Arm Circumference Skinfold Subscapular Skinfold Supra-Iliac Skinfold Mid-Axillary Skinfold Triceps
IBP Chest A-P Diameter Thorax Transverse Diameter Thorax Thoracic Circumference Acromial Height Biacromial Diameter	Non-IBP Chest A-P Diameter Manubrium A-P Diameter Substernal Sternal Length Substernal Circumference Thoracic Circumference Forced Inspiration Thoracic Circumference Forced Expiration

The study was structured to collect data on family groups, with the aim of measuring at least 200 parent-offspring pairs. In total, 845 people were measured, of whom 480 were children (from several months to 19 years of age) and 365 were adults. Most of the natives measured were from Camacani or surrounding localities. A few were from low altitude, and these were removed from the data analysis. The remaining respondents were arranged into familial aggregations. From these data came gross figures of approximately 265 father-offspring pairs, 290 mother-offspring pairs, and 205 midparent-offspring pairs.

Statistics Analyzed

Heritability estimates were made for stature, three IBP chest measurements, and the non-IBP chest measurements. Although the father-offspring regression was recommended as the method of choice for estimating heritabilities (Falconer 1972), the midparent-offspring regression was the primary method employed in this study. This was to avoid a possible underestimate of h^2 from father-offspring regression due to any illegitimacy that might exist in the population. Mother-offspring heritabilities, on the other hand, may be inflated by maternal effects. Thus in the midparent-offspring heritabilities, these possible sources of bias

should offset each other to some extent, and should best estimate the extent to which a genetic component might contribute to variation in chest dimensions (as well as stature) at high altitude.

Even though sib analysis yields heritability estimates that include dominance deviations and maternal effects, these were also computed. By comparison of the midparent-offspring heritabilities and the heritabilities derived from full sib intraclass correlations, the extent of nonadditive genetic variance can be estimated.

Finally, father-offspring heritabilities were calculated along with mother-offspring heritabilities. Comparison of these two estimates reveal whether maternal effects or illegitimacy are present or not.

All of the heritability estimates were calculated by the methods described in Table 1. A complication arose from the fact that there were unequal numbers of children in each family. Methods of handling this dilemma such as averaging of the offspring within one family or utilization of one child per family were discarded because they would reduce the amount of data, which would in turn increase the sampling error. A possible alternative would have been to include every parent-offspring pair as a single entity, but certain parents would have been weighted too heavily (due to many offspring), producing biases. The method chosen was somewhat laborious to calculate, but relatively unbiased and did not sacrifice any data. It uses a weighted least squares method, families of different size being weighted in proportion to the reciprocal of the variance of the estimate of regression that would be obtained from families all of that particular size. The weighting factors are based on an equation which incorporates information derived from intraclass correlations and unweighted regression coefficients (Falconer 1963).

Another problem lies in the fact that the people measured were of different ages and sexes. One method of overcoming this problem would have been to separate the sexes for both parents and offspring, then to have used growth curves to adjust all offspring measurements to a single age. This approach had two drawbacks. The first is that this also would have resulted in a reduction of the data. The second is that growth curves are highly uneven due to the presence of growth spurts at certain ages in some populations but not in others. In addition, longitudinal growth curves for the non-IBP measurements are unavailable. Another approach commonly taken is to make age and sex independent variables along with the offspring value, then to calculate multiple regression equations. However, this introduces two additional error terms into the model, since the ß-coefficients for the above have their own distribution. The preferred method is age-sex standardization of all measurements. Each individual's raw

measurements were converted into z-score deviations from the mean of the specific trait for the appropriate age and sex class. This introduces only one additional error term into the model. Standardization also has many advantages. If the sexes have unequal variances, standardization corrects this problem. It also removes differences between cohorts, thus allowing comparison of offspring over a wide range of ages.

The final statistic to be mentioned is a very important one--the standard error of the heritability estimate. As mentioned above (see Estimating Heritability) the magnitude of the standard error determines the credibility of the heritability estimate. For the purposes of this study the standard errors were calculated from the methods described in Falconer (1963).

RESULTS

Midparent Heritability Estimates

As mentioned above, all subjects who had ever lived at low altitude were removed from the study. This eliminated only about 5% of the sample, while ensuring its uniformity for the most important variable under study. The subjects were then arranged into family groups for computational purposes. Regressions of offspring values on midparent values were calculated. From the ß-coefficients came heritability estimates, which are shown in Table 2. These were listed according to the type of measurement: stature, sternal length, A-P diameters, transverse diameter, and circumferences. Along with the heritability estimates, standard errors are given. From these the probability that the $\hat{h}^2$ of the specific trait was equal to 0 (no additive variance), or 0.10 (little additive variance) was calculated.

Stature has a $\hat{h}^2$ of 0.51, and both p-values are highly significant. Sternal length has a somewhat lower heritability estimate of approximately 0.34, again significantly different from 0 and 0.10. The anterior-posterior depth of the chest at the superior margin of the sternum (A-P diameter manubrium) has a low $\hat{h}^2$ of 0.09, and is not significantly different from zero. Both A-P diameter thorax (mid-chest) and A-P diameter substernal (lower chest) have similar $\hat{h}^2$ estimates of 0.28 with moderate significance for $\hat{h}^2 = .10$. Transverse diameter has a low $\hat{h}^2$ of 0.145, but is not significantly different from $\hat{h}^2 = .10$. With the exception of thoracic circumference at forced expiration, which has a $\hat{h}^2$ of 0.26 with significance, the rest of the circumferences show low heritability estimates with little or no significance. Indeed, the $\hat{h}^2$ for substernal circumference (normal) is zero.

Table 2. Heritability Estimates Based on Midparent-Offspring Regressions
with Appropriate Hypothesis Tests

Trait	$\hat{h}^2$	Standard Error	P-value for $H_0{:}\hat{h}^2 = 0$	P-value for $H_0{:}\hat{h}^2 = .10$
Stature	0.509	0.135	<.0001	<.01
Sternal Length	0.343	0.123	<.01	<.05
Anterior-Posterior Diameter Manubrium	0.091	0.092	>.10	>.10
Anterior- Posterior Diameter Thorax	0.280	0.095	<.01	<.05
Anterior-Posterior Diameter Substernal	0.286	0.117	<.01	<.10
Transverse Diameter Thorax	0.145	0.103	<.10	> .10
Thoracic Circumference Normal	0.157	0.103	<.10	>.10
Thoracic Circumference-Forced Inspiration	0.123	0.123	>.10	>.10
Thoracic Circumference-Forced Expiration	0.264	0.102	<.01	<.10
Substernal Circumference Normal	0.000	0.107	>.10	>.10

Any $\hat{h}^2 \le 0$ was assumed to be 0.0.

Another way of viewing the data is given in Table 3.

Stature has the highest $\hat{h}^2$, followed by sternal length. These have moderate heritabilities. Next comes A-P diameter substernal, A-P diameter thorax, and thoracic circumference (forced expiration). The heritability estimates for these traits are slightly low

to moderate. For the remaining five measurements the heritability estimates can be considered low.

<div align="center">

Table 3. Rank Order of Heritability Estimates

</div>

Trait	$\hat{h}^2$	Trait	$\hat{h}^2$
Stature	0.509	Thoracic Circumference Normal	0.157
Sternal Length	0.343	Transverse Diameter Thorax	0.145
A-P Diameter Substernal	0.286	Thoracic Circumference-Forced Inspiration	0.123
A-P Diameter Thorax	0.280	A-P Diameter Manubrium	0.091
Thoracic Circumference Forced Expiration	0.264	Substernal Circumference Normal	0.0

Mother-Offspring and Father-Offspring Heritabilities

Table 4 gives the heritability estimates (along with the standard errors) obtained from regressions of offspring on mother and offspring on father. Midparent heritability estimates are shown for comparative purposes. The traits were listed in rank order of midparent $\hat{h}^2$ values.

For many of the traits, the midparent $\hat{h}^2$ falls between the maternal $\hat{h}^2$ and the paternal $\hat{h}^2$. This is to be expected, for as mentioned earlier the paternal $\hat{h}^2$ may be reduced due to illegitimacy in the population. The three traits where this does not occur have the lowest midparent $\hat{h}^2$, and statistical variability may account for this.

Of the 10 traits measured, three have appreciably higher maternal $\hat{h}^2$ than paternal or midparent $\hat{h}^2$; these are sternal length, A-P diameter thorax, and transverse diameter thorax. Maternal effects might then be operating in these traits to cause offspring to more resemble their mother. For A-P diameter substernal the maternal $\hat{h}^2$ is somewhat larger than the midparent $\hat{h}^2$, but much larger than the paternal $\hat{h}^2$. The latter estimate is quite small, and once again sampling deviation may be the causal element. As a result, it is uncertain whether there is an appreciable maternal effect for this trait.

Most standard errors for midparent, maternal, and paternal $\hat{h}^2$ values range from 0.09 to about 0.143. In only five estimates out of 30 are the standard errors above 0.15 (mentioned above

as the upper limit for validity), and all five are for paternal $\hat{h}^2$ on the bottom part of the rank order of $\hat{h}^2$. For the majority of the $\hat{h}^2$, the standard errors fall around 0.10 to 0.13, which is quite low considering the fact that large numbers of families must be measured to achieve that accuracy, yet only natives who were born and developed at high altitudes were used.

Table 4. Mother-Offspring and Father-Offspring Heritability Estimates

Trait	Mother-Offspring $\hat{h}^2 \pm$ S.E.	Father-Offspring $\hat{h}^2 \pm$ S.E.	Midparent-Offspring $\hat{h}^2$
Stature	0.542±0.135	0.425±0.140	0.509
Sternal Length	0.528±0.142	0.271±0.139	0.343
A-P Diameter Substernal	0.390±0.114	0.024±0.140	0.286
A-P Diameter Thorax	0.506±0.116	0.186±0.121	0.280
Thoracic Circumference-Forced Expiration	0.343±0.137	0.212±0.168	0.264
Thoracic Circumference-Normal	0.161±0.121	0.136±0.158	0.157
Transverse Diameter Thorax	0.267±0.119	0.110±0.159	0.145
Thoracic Circumference-Forced Inspiration	0.126±0.138	0.218±0.200	0.123
A-P Diameter Manubrium	0.189±0.106	0.160±0.143	0.091
Substernal Circumference	0.0±0.116	0.0±0.173	0.0

Comparison of Sib Analysis Heritabilities with Those Based on Other Relationships

Although a $\hat{h}^2$ estimate derived from sib analysis will have a substantial amount of nonadditive genetic variance and common environmental variance, in conjunction with more accurate methods it gives a rough idea of the magnitude of V_d, V_i, and V_{Ec} for the trait in question. Table 5 shows the heritability estimates derived from sib intraclass correlations for the 10 traits studied. Midparent and maternal heritability estimates cited above are also listed for comparative purposes.

**Table 5. Heritability Estimates Derived from Sib Analysis
with Comparative Estimates**

Trait	Sib Analysis $\hat{h}^2 \pm$ S.E.	Maternal $\hat{h}^2$	Midparent $\hat{h}^2$
Stature	0.429±0.117	0.542	0.509
Sternal Length	0.414±0.116	0.528	0.343
A-P Diameter Substernal	0.299±0.113	0.390	0.286
A-P Diameter Thorax	0.221±0.110	0.506	0.280
Thoracic Circumference-Forced Expiration	0.169±0.108	0.343	0.264
Thoracic Circumference-Normal	0.253±0111	0.161	0.157
Transverse Diameter Thorax	0.247±0.111	0.267	0.145
Thoracic Circumference-Forced Inspiration	0.332±0.114	0.126	0.123
A-P Diameter Manubrium	0.0±0.101	0.189	0.091
Substernal Circumference Normal	0.278±0.112	0.0	0.0

An immediately disturbing aspect of the results in Table 5 is that four of the traits (stature, A-P diameter thorax, thoracic circumference on forced expiration, and A-P diameter manubrium) have a sib $\hat{h}^2$ that is less than both maternal and midparent $\hat{h}^2$. For stature this deficit is not large and may just reflect sampling deviation. It was noted earlier that A-P diameter thorax calculated from mother-offspring regression differed markedly from that based on father-offspring regression (Table 4). The fact that the sib $\hat{h}^2$ for this trait is close to the midparent $\hat{h}^2$ suggests that the latter is quite possibly the most accurate estimate, and that the separate parental estimates were not accurate. For thoracic circumference (forced expiration) and A-P diameter manubrium, the various heritability estimates are not easily interpretable. Sternal length had maternal $\hat{h}^2$ > sib $\hat{h}^2$ > midparent $\hat{h}^2$. This indicates that some maternal effects are present, but with little or no nonadditive genetic variance. Sampling deviation might account for the differences between the maternal and sib $\hat{h}^2$. The same could be said for A-P diameter substernal, except that the sib $\hat{h}^2$ is close to the midparent $\hat{h}^2$. For transverse diameter the sib $\hat{h}^2$ is almost equal to the maternal $\hat{h}^2$, and both are larger than the midparent $\hat{h}^2$. Unlike the above traits, for transverse diameter the ordering of $\hat{h}^2$ values is as expected (sib $\hat{h}^2$ ≥ maternal $\hat{h}^2$ ≥ midparent $\hat{h}^2$). Maternal effects seem to be operating, and they explain the majority of the nonadditive variance.

Three of the traits (thoracic circumference normal, thoracic circumference on forced inspiration, and substernal circumference normal) have sib $\hat{h}^2$ > maternal $\hat{h}^2$ = midparent $\hat{h}^2$. This implies little or no maternal influence, but some nonadditive genetic variance. For substernal circumference normal though, the other $\hat{h}^2$ values are zero, and thus any genetic variance is highly improbable. Perhaps the high sib $\hat{h}^2$ can be attributed to other aspects of the common environment besides maternal effects.

The standard errors for all of the sib heritability estimates range from 0.10 to 0.12. These are quite low for studies of human populations.

Summary of Results

Table 6 summarizes the results discussed in the previous sections. As was mentioned above, the midparent value is the one that will be used in estimating heritability. The implications of these results will be discussed in the next section.

Table 6. Summary of Results for the Heritability Estimates

Trait	$\hat{h}^2$ *	Magnitude	Nonadditive Effects Present
Stature	.509	Moderate, significantly different from 0 and 0.10	Little or no effects
Sternal Length	.343	Moderate, significantly different from 0 and 0.10	Maternal effects
A-P Diameter Substernal	.286	Low to moderate, significantly different from 0 and 0.10	Slight maternal effects
A-P Diameter Thorax	.280	Low to moderate, significantly different from 0 and 0.10	Maternal effects
Thoracic Circumference-Forced Expiration	.264	Low to moderate, significantly different from 0 and 0.10	Slight maternal effects
Thoracic Circumference Normal	.157	Low, significantly different from 0	Nonadditive genetic variance
Transverse Diameter Thorax	.145	Low, significantly different from 0	Maternal effects, possibly some nonadditive genetic variance
Thoracic Circumference-Forced Inspiration	.123	Low, not significantly different from 0	Nonadditive genetic variance
A-P Diameter Manubrium	.091	Low, not significantly different from 0	Unclear
Substernal Circumference Normal	0	Low, not significantly different from 0	Unclear

* Midparent estimate

DISCUSSION

Validity of the Estimates

Whenever a human quantitative genetic study is undertaken, the first question that one should ask is, "Are the estimates credible?" This is because genetic studies of human populations operate under many restrictions which the animal or plant geneticist might not encounter. Consequently, the final gathering and analysis of data, no matter how well intended the experiment, might be inadequate or inappropriate.

The above caution applies directly to the present study. One of the goals of the experiment was to obtain standard errors for the heritability estimates that were less than 0.15. Out of a total of 40 heritability estimates, only five had standard errors greater than 0.15, and these were all paternal $\hat{h}^2$ with low values. For the most part, the standard errors were in the range of 0.10 to 0.13, thus achieving the above goal.

It had also been postulated that the maternal $\hat{h}^2$ should be higher than the paternal $\hat{h}^2$, and that the midparent $\hat{h}^2$ should fall somewhere between the two estimates. Eight of the 10 traits examined showed this trend. The sib $\hat{h}^2$ should have been the largest estimate obtained for a specific trait. However, this was the case for only three of the traits. In fact, for the majority of the traits, the $\hat{h}^2$ based on sib analysis did not show the expected pattern, and although certain inferences were drawn from them (Table 6, last column), these must be regarded with caution.

Taking into account all of the above statements, the results obtained should nevertheless be regarded as plausible overall. Caution should be taken as to specifics, though. For example, although it would be accurate to state that in the population studied sternal length has a moderate $\hat{h}^2$ or transverse diameter has a low $\hat{h}^2$, it would be speculative to state the two estimates as 0.343 and 0.145 respectively (Table 2). Taken together, the estimates give a general idea as to what part of the phenotypic variance is contributed by additive genetic variance. Even with all of the study's inherent limitations, it makes a major advance over the previous state of knowledge (see Review of Previous Studies).

Interpretations Arising from the Heritability Estimates

Aside from stature, the literature is sparse on heritability estimates for anthropometric measurements. Hewitt (1957) reports a sib correlation of 0.448 for skeletal maturity from the Oxford Child Health Survey. This would amount to a very high heritability, but dominance and environmental covariance could have inflated this estimate.

In a study of Belgian urban families (Susanne 1977), heritability estimates were obtained for 36 anthropometric traits. The only one comparable to those reported here was a $\hat{h}^2$ of 0.787 for sternal height. Mueller (1975) measured Colombian rural natives, and got a heritability estimate of 0.63 for biacromial breadth. Even though the comparative data are scarce, one point stands out: the previous estimates of heritability for skeletal traits included in this study were all high. Such is not the case in this study. The highest $\hat{h}^2$ obtained was for stature, the measurement that was not specifically part of the thoracic complex. For the chest measurements themselves the results can be divided into two categories: those showing low moderate to moderate heritabilities, which includes four measurements, and those exhibiting low heritabilities, which includes five measurements (Table 6). None of the traits in the second category are significantly different from $\hat{h}^2 = .10$.

There is some variation by type of measurement. Traits such as sternal length, A-P diameter thorax, and A-P diameter substernal which describe chest length and depth have the larger $\hat{h}^2$. The A-P diameter at the manubrium, which measures chest depth at the level of the clavicle, would not be included in the former category (indeed, its $\hat{h}^2$ is quite low). And with the exception of thoracic circumference (forced expiration), the rest of the traits which measure chest width and circumference have low heritability estimates. Thus the traits with the higher heritabilities are, interestingly enough, precisely those which more accurately describe the Andean thorax. Two examples point this out. Transverse diameter thorax and A-P diameter thorax are taken at the same level (midchest, specifically at the junction of the third and fourth segments of the sternum), but the former measures chest width while the latter measures chest depth. The respective heritability estimates are 0.145 and 0.280. Substernal circumference normal and A-P diameter substernal are both taken at the lower margin of the sternum. The respective heritability estimates are 0.0 and 0.286.

Nonadditive genetic variance seems to be appreciable in only two traits: thoracic circumference (normal) and thoracic circumference (forced inspiration). These are both measurements of circumference. Thus traits that measure chest length and depth not only seem to have the higher heritabilities, but also have most of the genotypic variance as additive (hence, simply inherited) variance.

Maternal effects and influence of common environment, which are so difficult to partition out from the genotypic variance, seem to be present in the traits that measure chest length and depth (Table 6). This is not necessarily a reason for their higher heritability estimates. By looking at Table 4, it will be noted that the midparent $\hat{h}^2$ are quite different from the maternal $\hat{h}^2$, and thus give a reasonable estimate of $\hat{h}^2$. If the midparent $\hat{h}^2$ were close to

the maternal $\hat{h}^2$, then quite possibly the former could have been partially inflated by maternal effects. As maternal effects can be nuclear, cytoplasmic, environmental, or a combination thereof (Nance et al. 1978), this represents another possible source of inherited variation that could make offspring resemble their female parents more.

The only departure from the above interpretation is for thoracic circumference (forced expiration). While the paternal and sib heritability estimates are low, the midparent and maternal heritability estimates are in the low to moderate range. Three possible explanations for this departure are: statistical deviation, inaccuracy of measurement, and appreciable maternal effects.

Extension of Results

The purpose of this study was to calculate heritability estimates in an attempt to determine the amount of genetic variation in the traits which describe the morphology of the thorax in Andean populations. As noted above, the conclusions drawn from previous studies conflicted with each other, some hypothesizing that there are genetic factors which shape the development of the thoracic complex in high altitude Andean populations, others suggesting that all differences between high- and low-altitude populations are attributable to direct environmental influences. After reviewing the results of this study it is understandable why that conflict was possible. The heritabilities calculated here were neither uniformly very high nor very low. It is clear that in stature, sternal length, A-P diameter thorax, thoracic circumference (forced expiration), and A-P diameter substernal both environmental and genetic factors contribute to the phenotypic variance. In the rest of the traits the amount of genotypic variance is low. Of all the traits studied, only two had $\hat{h}^2$ greater than 0.30: stature and sternal length. This finding of generally low heritability estimates points toward the possibility of more substantial environmental influence on variation in chest traits than on variation in stature.

The analysis here does help in interpreting the results from previous studies. It was noted in some studies that the Andean thorax was large relative to stature. If stature, with a $\hat{h}^2$ of 0.542 were undergoing selection for smaller size while chest traits were experiencing little change due to selection, then the end result of this allometric change would be chests larger relative to stature, agreeing with the results found by Beall and others (1977). However, a similar allometric change could be brought about by selection acting with greater intensity on chest dimensions than on stature. This second alternative could also help explain the

relatively low heritabilities of chest dimensions estimated here, since directional selection reduces additive genetic variation.

The hypotheses forwarded by Frisancho (1969, 1975), Frisancho et al. (1975), and Lahiri et al. (1976) suggest that the adaptations of the high-altitude natives are purely within-generational developmental acclimatizations to the environment. Yet a strictly environmental causation would not explain the contention of Hurtado (1971), that no matter how long a migrant from low altitude lives at high altitude, he will never become as fully adapted as the native born and bred at high altitude. Moreover, the findings by Hoff (1974) that first-generational offspring of migrants from high altitude still exhibit larger chest dimensions cannot be supported by a strictly environmental causation of chest size. The key to unraveling this dilemma lies in the actual shape of the Andean thorax. As was mentioned in the introduction, the thorax is longer and deeper than the thorax characteristic of low-altitude populations. It is worth noting that the three chest traits (sternal length, A-P diameter thorax, and A-P diameter substernal) which contribute most directly to the observed differences between high- and low-altitude populations are also those with the highest heritabilities estimated here. If the rank order among the heritabilities in this population had been the same in the past as it is at present, then the traits with the higher heritabilities would have been those more responsive to selection for larger chest size. This response to selection in high-altitude populations could have contributed to their differentiation from low-altitude groups.

If differences in chest size and shape between high- and low- altitude Andean populations are attributable in some part to evolutionary changes, then it is possible that those traits that changed most markedly were simply the ones in which there was sufficient genetic variation on which selection could have acted. However, it is also possible that increases in thoracic volume resulting from increases in chest depth and length were favored because they interfered with other functions less than would have been the case for increases in chest width. For example, increases in chest width might have required changes in the growth of bones in the shoulder girdle, while increases in chest depth and length could have been accomplished by developmental changes substantially confined to the ribs and sternum. Of course, these alternatives are by no means mutually exclusive, and assessment of their explanatory value must in any case await further research.

CONCLUSIONS

Heritability estimates were made on 10 anthropometric traits for a high-altitude Aymara population in order to assess the extent to which variations in the thoracic complex have any heritable components. Except for stature and three chest dimensions, the heritabilities estimated were quite low. From these results and those of previous studies, it was postulated that a significant environmental component could be involved in adaptation to the Andean environment.

Some earlier studies had pointed towards a possible heritable component in the Andean thorax. Consistent with these studies is the finding here that the three chest traits with the highest heritabilities were the ones that most accurately defined the Andean thorax: sternal length, A-P diameter thorax, and A-P diameter substernal. These three traits are measures of chest length and depth. Other measurements in the same region but not reflecting length or depth had lower heritabilities.

From the results reported here it can be concluded that there is, at present in this population, sufficient heritable variation on which selection could act to influence thoracic size, particularly the length and depth of the chest. If this situation also existed in the past, then it is possible to understand how selection might have acted to increase the space available for lung expansion in an environment characterized by the pervasive stress of hypoxia.

CHAPTER 3

THE RELATIONSHIP OF FORCED VITAL CAPACITY TO MORPHOLOGY
AND FAT-FREE MASS IN HIGH-ALTITUDE ADULT AYMARA MEN

Kellie Lynn Whittaker

INTRODUCTION

Forced vital capacity (FVC) is strongly correlated with thoracic morphology in high altitude Andean populations (Hurtado 1932a, Garruto 1969, Frisancho et al. 1973, Mueller et al. 1978c, Malik and Singh 1979). This correlation may be thought of as a structural association since thoracic dimensions and volume represent limits which lung dimensions and volumes may approach but never reach. As tissue oxygen supply is the paramount problem under hypoxic conditions (Goddard et al. 1967), all components of the oxygen transport/use system in high altitude natives, including lung volume, ought to show functional associations with one or more biological parameters reflecting oxygen need. Need for oxygen should be directly proportional, at rest, to the amount of tissue requiring oxygen, and during activity, to the amount of work done by the body. In the latter case, body weight would be expected to be an important factor, since total body weight makes up the largest part of the workload in many activities.

FVC is linearly related to maximal oxygen consumption (VO_{2max}), in sea-level subjects (e.g., Astrand 1952). VO_{2max} in turn shows a fairly high correlation with weight (Harrison et al. 1977). It might be expected that FVC would also be associated with weight. However, Boyce et al. (1974) found that after height variation had been controlled for in high-altitude Quechua men, weight exerted little statistical effect on FVC.

Weight can be separated into two components, fat mass and fat-free mass (FFM). Since fat is metabolically relatively inert when compared to tissues such as liver and muscle (Rony 1940), variation in the amount of fat will affect total body weight but not the metabolically active mass of tissue. While FFM incorporates tissues such as liver in addition to smooth and striated muscle, FFM may be used as an estimate of the active muscle mass if the assumption is made that the various internal organs and tissues comprise some constant percentage of body weight. Strenuous work or exercise considerably increase the metabolic requirement for oxygen. This increase in oxygen requirement is due to increased oxygen consumption by the active muscle

mass. Under conditions where oxygen is the limiting factor, FVC may be associated with the amount of FFM rather than total body weight.

The purpose of this paper is to examine the relationship of FVC and thoracic and overall body morphology to estimates of fat-free mass in a Peruvian group of high altitude born and resident Aymara men.

METHODS AND TECHNIQUES

Population and Sample

The study population consists of Aymara Indians residing in the village of Camacani, Departamento de Puno, Peru. Camacani has approximately 2100 residents, who are virtually all Aymara speakers. The village is located in an area where altitude ranges from 3904 to 4160 m above sea level (Brigada Tecnical de Campo 1976). Agriculture is the main livelihood of the community, which is situated on the shore of Lake Titicaca. Although linguistic barriers cannot necessarily be construed as reproductive barriers, the fact that Camacani appears to have very few residents of European ancestry suggests that little European-Aymara admixture has occurred. Furthermore, the work of Cruz-Coke et al. (1966) and Reynafarje et al. (1965) on blood groups (ABO system) has shown that the Aymara of Puno are very similar to the Aymara of Arica, Chile, whose Caucasian admixture has been estimated at 8.9% (Cruz-Coke et al. 1966).

As part of a survey conducted in 1978, anthropometric and health data were collected for 773 people, including 166 men, 181 women, 256 boys, and 170 girls. Neither Quechua speakers nor persons born or ever resident at altitudes lower than about 3800 m above sea level were included in the sample. The subsample used for this study consists of the 83 adult males for whom FVC was measured. Adulthood was defined as greater than 20 years of age, the earliest age at which all anthropometric values showed no significant differences from adult mean values ($p < .05$). Adult mean values were computed from all male subjects 25 years of age or older. These estimates should be conservative, since Frisancho and Baker (1970) have shown that virtually all growth is finished by age 18 in high altitude Quechua males. Forced vital capacity was measured on a random sample of men whose responses to a health questionnaire indicated no evidence of respiratory disease. The majority of the measurements (approximately 95%) were taken in a room which was converted into a laboratory at the Centro Experimental Camacani, an agricultural experiment station run by the Universidad Nacional Tecnica del Altiplano. Occasionally, if an individual expressed desire to participate but was unable to

travel to the laboratory, the subject was measured at home. Adult participants volunteered for the study.

Measurement Techniques

In total 20 anthropometric measurements were taken, 14 according to standard International Biological Programme (IBP) techniques (Weiner and Lourie 1969) and 6 additional measurements. Non-IBP measurements are defined as follows:

1. Antero-posterior diameter at manubrium: measured horizontally between the notch on the manubrium and the vertebral column.

2. Antero-posterior diameter substernale: measured horizontally between the most inferior point of the sternum and the vertebral column.

3. Sternal length: measured from the superior aspect of the manubrium to the most inferior point of the sternum.

4. Substernale circumference: measured at the most inferior point of the sternum, at right angles to the axis of the body, at the end of a normal expiration.

5. Thoracic circumference - forced inspiration: measured in the same way as the IBP definition of chest circumference, but at maximal inhalation.

6. Thoracic circumference - forced expiration: measured in the same way as the IBP definition of chest circumference, but at maximal exhalation.

Forced vital capacity was measured using a 9-liter Collins wet spirometer according to the methods of Consolazio et al. (1963) and subsequently converted to BTPS. All spirometric measurements were taken by the same experienced technician.

Five additional indices of thoracic morphology were calculated from direct anthropometric measurements, including chest expansion, chest volume at the end of a normal exhalation, chest volume at maximum inhalation, chest volume at maximum exhalation, and chest volume expansion. Chest expansion, a measure of flexibility, was calculated by subtracting thoracic circumference at maximum expiration from thoracic circumference at maximum inspiration. All chest volumes were calculated by treating the chest as a cylinder and using the respective chest circumference (normal chest circumference, circumference at maximum inspiration or circumference at maximum expiration) to calculate the area of the "circles" bounding the cylinder. Chest volumes, as upper limits to lung volume, were then calculated by multiplying areas of the respective "circles" by sternal length.

Fat-Free Mass: Definition and Calculation

Fat-free mass (FFM) is defined as the difference between total body weight and the weight of all fat, and provides a good measure of metabolically active tissue (Behnke 1953). It should be noted that FFM has occasionally been confused in the literature with a slightly different measure of metabolically active tissue, lean body mass. Behnke (1953) defines lean body mass as "the difference between gross weight and the weight of excess fat," and specifies that lean body mass incorporates a constant percentage of adipose tissue that he calls essential fat. Since the amount of "essential" fat in the lean body mass is not precisely known (there are varying estimates in the literature) and since fat is relatively inert metabolically, FFM is the more precise measure of metabolically active tissue.

Fat-free mass may be estimated by one of four methods: 1) total body water, 2) densitometry, 3) specific gravity, calculated from height and weight rather than from densitometry, and 4) skinfold measurements. Although estimates of FFM from total body water and densitometry agree closely, these measurements were not taken in the population under study. Fat-free mass estimates from specific gravity calculated from height and weight measurements (e.g., Cowgill 1957) have a lower correlation with estimates of FFM from densitometry and total body water than do FFM estimates from skinfolds (Womersley and Durnin 1977). Skinfold measurements appear to provide the best possible means available by which to estimate FFM. Lohman (1981) concluded that any of several combinations of two or three skinfolds were statistically equivalent for the purpose of predicting body density in young adult males, and that using more than three skinfolds did not improve accuracy. Although Lohman (1981) listed several combinations of skinfolds which were statistically equivalent, only one combination could be applied to this study since not all of the skinfolds Lohman measured were included. Therefore, Lohman's (1981) equation using triceps and suprailiac skinfolds (derived from college-age males, population not specified) was used to predict body density:

Density = 1.0855 - 0.00091 x Triceps skinfold - 0.00065 x Suprailiac skinfold,

where skinfolds are measured in millimeters. The amount of variation in density associated with these variables (R^2) in the original population was 0.76 and the standard error of the estimate was 0.0052. From body density an estimate of percent fat was calculated using Siri's (1961) formula, which assumes a density of 0.900 gm/cc of fat in the living body and a density of 1.100 gm/cc for the FFM:

$$\% \text{ Fat} = \left(\frac{4.95-4.50}{D} \right) \times 100.$$

Fat-free mass was then calculated according to the following equation:

$$\text{FFM} = (1 - \% \text{ Fat}) \times \text{Weight}.$$

Statistical Procedures

All computer programs used in the analysis of data for this study were written in SAS (Statistical Analysis System), a widely available statistical package. Means were calculated to provide descriptive statistics for the population. Correlation analysis was used to test the strength and direction of the relationship between FVC and each independent variable in turn. The means and correlations were calculated using the SAS procedures MEANS and CORR respectively. Regression analysis was then used to investigate the linear relationship of FVC to various combinations of independent variables. Regression was done using one of two SAS procedures, depending on the goal of the particular regression analysis. To evaluate any single given model, the SAS procedure GLM (General Linear Model) was used. To obtain the best set of predictor variables for $p \geq 1$ (where p = number of independent variables in the model), the SAS procedure STEPWISE, with the MAXR option, was used. Most statistical methods for obtaining the best set of predictor variables either do not remove a variable from the model once entered or may remove a variable if it does not meet some specified level of significance. The MAXR option finds the best model at each level of p by comparing each variable already in the model to each variable not in the model, in order to determine which variable will produce the greatest increase in R^2 (SAS User's Guide 1979).

RESULTS

Means

Mean values for all variables are presented in Table 1.

Table 1. Means for Adult Aymara Men (N = 83)

Variable	Mean	Standard Deviation	Minimum Value	Maximum Value
FVC[a]	4.920	0.983	3.096	8.944
Age	40.5	14.7	20.0	81.0
Weight[b]	58.8	6.0	46.9	76.9
Height[c]	161.4	5.9	150.1	178.0
Sitting height[c]	85.1	3.5	76.5	94.5
Acromial height[c]	56.5	3.3	49.8	64.6
Biacromial diam.[c]	36.8	2.6	28.9	42.7
Biiliac diam.[c]	28.2	1.8	24.2	35.9
Sternal length[c]	21.1	2.4	14.4	29.7
A-P diameter—manubrium[c]	16.1	1.9	13.4	29.3
A-P diameter—thorax[c]	21.6	1.5	16.0	25.3
A-P diameter—substernale[c]	21.9	1.5	18.9	25.9
Transverse diam.[c]	29.2	2.1	19.7	35.9
Thoracic circ.—normal[c]	92.2	4.4	79.0	103.5
Thoracic circ.—inspir.[c]	96.5	4.3	86.0	106.5
Thoracic circ.—expir.[c]	89.7	4.2	81.2	101.0
Substernale circ.[b]	87.6	4.1	79.5	99.2
Arm circ.[c]	25.7	1.7	19.9	29.8
Subscapular skinfold[d]	11.7	4.4	4.5	32.5
Suprailiac skinfold[d]	8.3	4.8	3.0	25.0
Midaxillary skinfold[d]	6.7	2.9	2.5	17.5
Triceps skinfold[d]	11.9	5.4	4.0	30.0
Density	1.069	0.007	1.045	1.080
Percent fat	13.0	3.1	8.4	23.6
Fat-free mass[b]	51.1	4.8	42.4	65.1
Chest volume[a]	10.753	1.660	5.656	14.305
Chest volume at inspir.[a]	15.676	2.256	10.599	20.928
Chest volume at expir.[a]	14.581	2.107	9.594	18.427
Chest volume expansion[a]	1.095	0.405	0.210	2.048

[a]in liters, [b]in kilograms, [c] in centimeters, [d] in millimeters

Correlation Analysis

Results of the correlation analysis are presented in Table 2. These results are summarized as follows:

1. Forced vital capacity was significantly correlated with all variables measuring general body and trunk morphology.

2. Of 12 measures of thoracic morphology 4 were significantly correlated with FVC: transverse diameter, maximum thoracic circumference, chest expansion, and chest volume expansion.

3. FVC did not correlate significantly with any measures of fatness, which reflect the amount of non-metabolically active tissue in the body.

4. FVC showed a significant negative correlation with age and a significant positive correlation with FFM, a measure of metabolically active tissue.

Table 2. Correlations with FVC for Aymara Men

Measures of General Body and Trunk Morphology		Measures of Thoracic Morphology	
Height	0.62***	Sternal length	-0.06
Weight	0.39***	A-P diameter--manubrium	0.02
Sitting height	0.52***	A-P diameter--thorax	-0.03
Acromial height	0.52***	A-P diameter--substernale	-0.13
Biacromial diameter	0.27*	Transverse diameter	0.30**
Biiliac diameter	0.27*	Thoracic circ.--normal	0.02
		Thoracic circ.--inspir	0.37***
Measures of Fatness		Thoracic circ.--expir.	0.08
		Substernale circ.	0.04
Arm circumference	0.07	Chest expansion	0.56***
Subscapular skinfold	-0.10	Chest volume	0.10
Suprailliac skinfold	0.12	Chest volume at inspir.	0.17
Midaxillary skinfold	-0.07	Chest volume at expir.	-0.01
Triceps skinfold	0.04	Chest volume expansion	0.54***
Density	-0.08		
Percent fat	0.08		
		Measures of Metabolism	
		Age	−0.59***
		FFM	0.40***

$*p < .05, **p < .01, ***p < .001$

Regression Analysis

The results of the regression analysis performed in order to obtain the best predictors of FVC are presented in Table 3. This table shows the best possible regression model for FVC, at each level of p, on all measured and calculated anthropometric variables, excluding FFM.

Table 3. Best Regression Model for Aymara Men, for Dependent Variable FVC (where p is the number of independent variables included).

Estimates of Regression Coefficients

Best Model	Y	Age	Height	Acromial Height	Chest Expansion	R^2	S. D.
Height	-12.096		0.105			0.40	0.764
Height	-10.356		0.087			0.56	0.661
Chest Expansion					0.131		
Age	-7.526	-0.019				0.62	0.618
Height			0.076				
Chest expansion					0.131		
Age	-7.938	-0.018				0.64	0.603
Height			0.063				
Acromial height				0.046			
Chest expansion					0.121		

Height was the best single predictor of FVC, with an R^2 of 0.40. When chest expansion was added to the model, the R^2 increased to 0.56. The best three-variable model contained the variables age, height, and chest expansion, yielding an R^2 of 0.62, whereas the addition of acromial height gave an R^2 of 0.64 and constituted the best four-variable model. The most parsimonious model was the three-variable model, referred to hereafter as the best anthropometric model.

The variables in the best anthropometric model (age, height, and chest expansion) may be thought of as representing structure rather than function; height represents skeletal size and chest expansion refers to thoracic flexibility. While it is generally agreed that basal metabolism decreases with age, a given amount of work requires a given amount of energy (and hence oxygen), regardless of basal metabolism. It seems likely that the decrease in FVC associated with age in this population is due, at least in part, to loss of thoracic expansibility rather than to any decrease in metabolic requirement for oxygen.

Fat-free mass may be thought of as representing function rather than structure, since it is an estimate of the active muscle mass. To evaluate whether FFM made any significant

contribution, it was added to the best anthropometric model. This created a four-variable model but no increase in R^2. Therefore, the null hypothesis (that addition of FFM as an independent variable does not significantly increase the accuracy of the model) cannot be rejected on the basis of these results.

The presence of multicollinearity (intercorrelations between independent variables) may obscure the relationship between FVC and FFM. Intercorrelations among the independent variables in the best anthropometric model and between those variables and FFM are presented in Table 4.

Table 4. Intercorrelations Among Selected Independent Variables.

	Age	Height	Chest Expansion
Age	——	——	——
Height	- 0.32**	——	——
Chest Expansion	- 0.47***	0.25*	——
FFM	- 0.13	0.71***	0.11

*$p < .05$, **$p < .01$, ***$p < .001$

The relationship R^2 does not change when FFM is added to the regression equation as an independent variable; it would appear that R^2 is a useful tool when making gross distinctions between models, but in order to make decisions about statistical significance, a statistical test is required. Before conducting such a test to determine whether FFM exerts a statistically significant effect on FVC, a brief discussion of the theory underlying the test will be given.

In multiple regression, the general linear relationship between the independent variable and the dependent variables is expressed as follows:

$$Y = B_0 + B_1X + B_2X + B_3X + \ldots + B_kX_k$$

where Y is the dependent variable, X_k represents a given independent variable, and B_k is the regression coefficient (beta coefficient) associated with a particular independent variable X_k (Neter and Wasserman 1974). The value of a given beta coefficient (e.g., B_2) indicates that a one-unit increase in X_2, holding all other independent variables constant, will change Y by an average of B_2 units. If Y does not respond to any change in X_k (that is, if $B_k = 0$), then there is no relationship between Y and X_k. To formally test the proposition that no relationship exists between Y and X_k, the hypothesis that B_k is not significantly different from zero must be

examined. This is done by means of a t-test. If the absolute value of t(observed) is less than or equal to t(tabulated), then H_0 cannot be rejected; B_k does not differ significantly from zero. If the absolute value of t(o) is greater than t(t), H_0 is rejected; B_k is significantly greater than zero, meaning X_k exerts a statistically significant effect on Y (Neter and Wasserman 1974).

The regression equation used in this study may be stated as follows:

$$FVC = B_0 + B_1 Age + B_2 Height + B_3 Chest\ expansion + B_4 FFM.$$

When this equation was computed by SAS, B_4 was estimated as 0.008, and the standard error of the estimate was given as 0.020 (Table 5). The observed value of t (0.37) was much less than the tabulated value of t (1.665), for a one-tailed significance level of 0.05 and 78 degrees of freedom. Therefore, H_0 cannot be rejected and B_4 has not been found to be significantly different from zero. By extension, then, FFM has not been found to exert any statistically significant effect on FVC. It should be emphasized again that all other independent variables were assumed to be held constant in order to conduct the test; in other words, the fact that height and FFM show a strong correlation is taken into account.

Table 5. Estimates of Regression Coefficients and t-Values
(observed and tabulated) for Independent Variables in the Model
$FVC = B_0 + B_1 Age + B_2 Height + B_3 Chest\ expansion + B_4 FFM.$

Parameter	B_k	Estimate of B_k	Std. Error of Estimate	t(obs.)	t (tab.)	H_0 : $B_k=0$
Intercept	B_0	-7.110	2.262	-3.14	1.665	Rejected
Age	B_1	-0.019	0.005	-3.59	1.665	Rejected
Height	B_2	0.072	0.017	4.11	1.665	Rejected
Chest Expansion	B_3	0.130	0.034	3.77	1.665	Rejected
FFM	B_4	0.008	0.020	0.37	1.665	Accepted

DISCUSSION AND CONCLUSIONS

In this study, the relationships between FVC and morphology and between FVC as an estimate of oxygen intake and FFM as an estimate of oxygen need were examined, using a sample of high-altitude Aymara men.

Correlation analysis indicated that significant associations existed between FVC and all measures of general body and trunk size as well as age and FFM. Further, FFM showed a slightly higher correlation with FVC than did total body weight. Four out of 12 measures of thoracic morphology correlated significantly with FVC: transverse diameter, chest expansion, chest expansion volume, and thoracic circumference at maximum inspiration. These parameters have also been found to correlate significantly with FVC in Quechua (Frisancho 1969, Garruto 1969, Hoff 1972). No measures of fatness, such as subscapular skinfold, were significantly correlated with FVC.

Regression analysis indicated that the model which explained the most variation in FVC contained the variables age, height, and chest expansion, with an R^2 of 0.62. The addition of FFM as an independent variable to the best anthropometric model produced neither an increase in R^2 nor a decrease in standard deviation. A t-test conducted on the regression coefficient associated with FFM showed that this regression coefficient was not significantly different from zero, implying that FFM as an independent variable had no effect on FVC.

The question arises as to whether assumptions made in the process of constructing the regression model, using FVC as the dependent variable, were valid. First, the assumption was made that height measured body (or skeletal) size and therefore represented structure rather than physiological function. While height does measure skeletal size, the amount of skeletal muscle should also be proportional in some degree to skeletal size. The amount of skeletal muscle has been shown to be strongly correlated with VO_{2max} (Mathews and Fox 1976). Height may, therefore, provide an indication of function as well as structure.

Second, it was implied that FFM was a better indicator of muscle mass than was height, since FFM was used to estimate metabolically active tissue. This cannot be proven, as neither muscle mass itself nor the relationships between muscle mass and FFM, and muscle mass and height were directly measured in this study.

Further, the fact that FFM was estimated by an equation derived from a different population than the one described in this study may be affecting the results. The validity of using a regression equation to predict FFM for individuals outside the group from which the equation was originally derived, and particularly since the original group was not perfectly described by the equation ($R^2 < 1.000$), is always suspect.

Alternatively, the assumption that FVC may be associated with a parameter as relatively variable as muscle mass (compared with thoracic dimensions, for instance) may not be valid. Several studies have shown that the enlarged FVC characteristic of high altitude Andean natives appears to be acquired developmentally (Lahiri et al. 1976, Frisancho et al.

1973, Frisancho 1975). Interestingly, normal aerobic capacity at altitude also appears to depend on developmental acclimatization to high altitude (Frisancho et al. 1973, Frisancho 1975). In fact, data presented in Figures 1-2 seem to suggest a relationship between FVC and VO_{2max}.
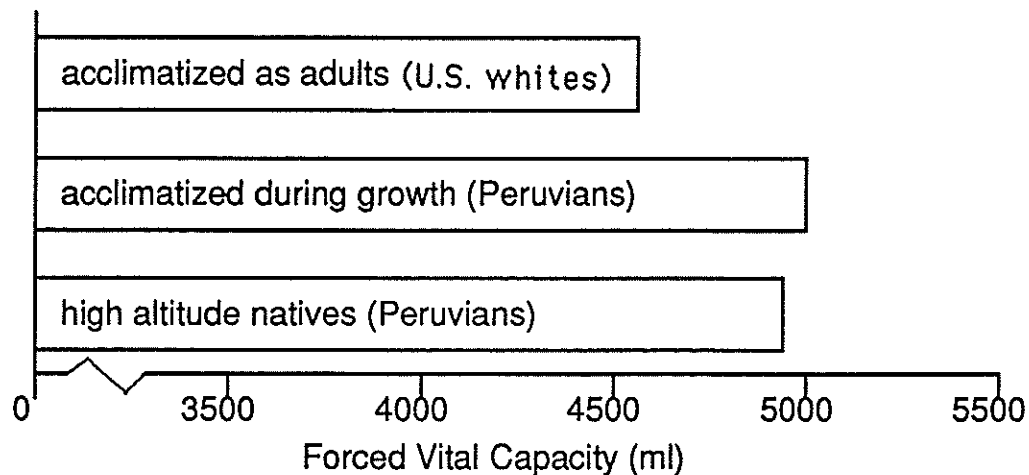

Figure 1. Comparison of FVC of high altitude natives, Peruvians acclimatized to high altitude during growth, and Americans acclimatized to high altitude during adulthood (adapted from Frisancho 1981).
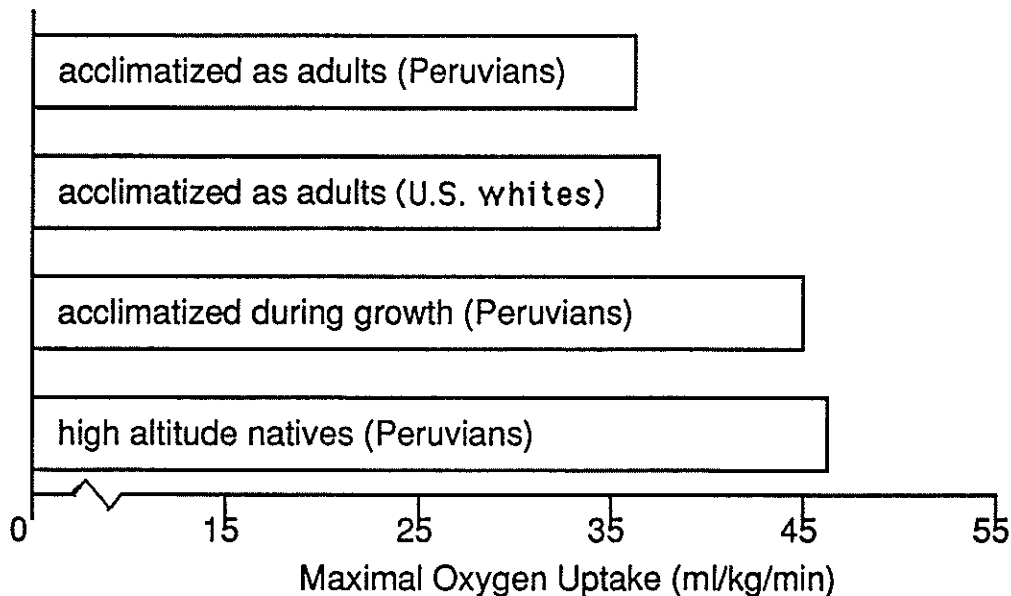

Figure 2. Comparison of aerobic capacity of high altitude natives, Peruvians acclimatized to high altitude during growth, Americans acclimatized to high altitude during adulthood, and Peruvians acclimatized to high altitude during adulthood (adapted from Frisancho 1981).

Those individuals having relatively higher aerobic capacities (high altitude natives and sea level natives acclimatized during growth) also had relatively higher FVCs than did United States whites or sea level natives acclimatized as adults (although data for the latter are not presented in Figure 1, Frisancho's 1981 paper specifically mentions these subjects). Although these data are sketchy and indicate only the possible direction of a relationship between FVC and VO_{2max}, they do not contradict Astrand's (1952) finding that FVC in a Swedish population was linearly related to VO_{2max}.

These results suggest that there is a limit to the potential increase in physiological efficiency of extracting and transporting oxygen, and when this limit is reached, the potential oxygen available (i.e. air volume in the lungs) at a given time must be increased. In the sea level native exposed to high altitude this is accomplished in part by an increase in respiratory rate, which serves to move the same amount of air into the lungs but at increased frequency. The high altitude native, on the other hand, does not show increased respiratory rate (long-term exposure to altitude seems to decrease sensitivity of the hypoxic chemoreceptors; see Lahiri et al. 1976, Severinghaus et al. 1966). As increased demand is not met by increased respiratory rate, it would seem logical that the volume of air in the lungs must increase to maintain an adequate supply of oxygen. The relationship of FVC to VO_{2max} might, therefore, reflect the minimum amount of air needed to guarantee a sufficient supply of oxygen to the body, even during maximum stress.

The response of humans to hypoxic stress is complex, however. It may be an oversimplification to attempt to find a functional association for FVC when in fact the larger lung volumes seen in high altitude natives are part of an array of interrelated and interdependent physiological reactions to hypoxia. As Frisancho (1975) has pointed out, functional adaptations to hypoxia may occur through changes, not only in FVC, but also in many other factors, such as: 1) pulmonary ventilation, 2) lung volumes and pulmonary diffusing capacity, 3) oxygen transport in the blood, 4) diffusion of oxygen from blood to tissues, 5) utilization of oxygen at the tissue level, or by some combination of these factors.

In summary, FVC was significantly correlated with all measures of general body and trunk size, and with four indices of thoracic morphology, for a sample of Aymara men born and resident at high altitude. Although FVC was significantly correlated with FFM, regression analysis indicated that there was no significant relationship between FVC and FFM in high altitude born and resident Aymara men. It was suggested that a more fruitful avenue of investigation might be to examine the relationship between FVC and VO_{2max} in high altitude populations.

CHAPTER 4

COMPARISON OF GROSS BODY MORPHOLOGY IN ADULT MALE QUECHUA AND
AYMARA LIVING ON THE SHORES OF LAKE TITICACA, PERU

David S. Lincoln

INTRODUCTION

Sources of genetic variation between human populations can be most accurately assessed in closely related populations which display physical differences. The Quechua and the Aymara of highland South America are related culturally (Bennett 1946) and genetically (Rothhammer and Spielman 1972), and are therefore suitable groups for a study of interpopulation genetic variation.

That there is consistent morphological variation between the Quechua and the Aymara has not been well documented. In 1980, Eckhardt gathered data on adult male Quechua and Aymara living on the shores of Lake Titicaca, Peru. The data consisted of the anthropometric variables comprising the IBP full list. Of 38 univariate comparisons, 14 were statistically significant ($p<.05$) with the Aymara having the larger mean value in 13 of the significant comparisons (Eckhardt et al. 1982). This study was important because the data were gathered on populations living in the same environment, thus controlling for the effects of altitude and climate.

Previous studies were not designed with the comparison of Quechua and Aymara populations as the primary goal. Anthropometric data on a number of Quechua and Aymara populations are available from published sources, but these data are usually limited to height, weight, and a small set of measurements chosen for the specific study. The value of these comparisons is limited because the number of variables is too small to give a complete picture of body build, and the populations utilized are living in environments differing in a number of ways, including altitude and climate. Eckhardt et al. (1982) compared the stature, weight, and two chest dimensions of Peruvian Quechua and Aymara children and young adults from Nuñoa and Camacani, respectively. The Aymara were found to be taller and heavier, with larger transverse chest diameters. In general, the Camacani Aymara live at lower altitude than the Nuñoa Quechua (about 3900 vs. 4000-4500 m above sea level). Camacani is on Lake Titicaca, in an environment that is wetter and has less diurnal variation in temperature than the puna environment of Nuñoa. Stinson (1980) studied the growth of Aymara children living in

Ancoraimes, Bolivia, and found them to have greater stature and weight but smaller chest dimensions than Quechua from Nuñoa, Peru. Ancoraimes is also located in the more moderate environment along Lake Titicaca.

In a study of factors affecting weight and length of neonates in Bolivia, Haas et al. (1980) found no statistically significant differences in stature, muscle area, or fat between Indian mothers from Santa Cruz (400 m above sea level), most of whom were Quechua, and Indian mothers from La Paz (3600 m), most of whom were Aymara. The only significant difference between Quechua and Aymara was in birth weight of male infants, with the Aymara having the lower mean value. This difference was attributed to the effects of altitude. Mueller et al. (1978b) studied variables associated with lung function in a sample of Chilean Aymara living on the altiplano in the Department of Arica. These researchers found that the expiratory volumes and vital capacities of male children approximated those of the Quechua. Patterns of precipitation are similar in the two regions, with somewhat greater diurnal variation in temperature on the Arica altiplano. Before the Quechua and the Aymara can be used in a study of genetic variation, consistent morphological variation between the groups should be documented and the source of any observed variation should be identified. Because the univariate comparisons performed by Eckhardt et al. (1982) have limited explanatory power, multivariate analysis of the Lake Titicaca data set was undertaken (Lincoln and Eckhardt 1984).

In multivariate analysis, each individual is regarded as a single observation consisting of measurements on a series of variables; then the biological unity of the individual is preserved. The covariance structure of these variables can provide biologically meaningful information. Multivariate techniques such as factor analysis and principal components analysis divide the total variance of a data set into a limited number of constituent parts based on the covariation among the measured variables. As a result, the relationship between the measured variables is clarified in a biologically meaningful way (Howells 1951). For the present study, principal components analysis was considered the most appropriate method because the procedure may be used to divide the total variance into independent components without *a priori* theoretical justification. Principal components represent axes of variation which can be tested for group differences, in this case between the Quechua and Aymara populations.

The specific aims of this analysis are twofold: 1) to investigate morphological patterning in a combined sample of Quechua and Aymara using principal components analysis, and 2) to test the principal components for differences between these two populations.

MATERIALS AND METHODS

The Sample

The sample was drawn from Quechua and Aymara populations living on the shores of Lake Titicaca in and around the villages of Coata and Camacani, respectively. The lakeshore region is approximately 3750 m above sea level, and is characterized by moderate climatic variation. The rainy season begins in November and extends through March, with an average monthly rainfall of 7.5 cm.; the temperature may range from 20° C to -5° C during this period. The dry season begins in April and extends through October, with an average monthly rainfall of 2.0 cm. and temperatures ranging from 21° C to -13° C (Stinson 1980).

The study populations consist largely of peasant agriculturalists. Potatoes and quinoa (*Chenopodium quinoa*) are the chief agricultural staples and mutton is one common source of protein in the diet. These foods are supplemented by tubers, grains, fish, and cheese. The region and its inhabitants have been described in detail elsewhere (Forbes 1870, Eckhardt and Kramer 1980, Eckhardt et al. 1982). The analysis was based on a combined sample of 20 Quechua and 20 Aymara adult males. The subjects were identified according to two criteria: 1) location of current residence and 2) first language spoken as a child.

Variable Choice

Data were available on the 38 anthropometric variables comprising the IBP full list. The data were gathered in order to describe body build in the lakeshore Quechua and Aymara groups; additional variables were computed from these data. The initial principal components analysis was based on a pooled correlation matrix of 32 variables (Table 1). Certain measurements were excluded from the analysis; there were various reasons for these exclusions. For example, Howells (1951) recommended that variables which may contain disparate growth centers be excluded from factor analyses because the intercorrelation between these and other variables may result in ambiguous factors. Such variables also duplicate information. Accordingly, the following variables were excluded from the analysis: sitting height, height of anterior superior iliac spine, total arm length, suprasternal height, and total leg length. Height and weight were retained as measures of overall body size. Height of tibiale and upper arm circumference (contracted) were dropped because they were highly correlated with lower leg length and upper arm circumference (relaxed), respectively. The distributions of the variables in the combined sample were examined for deviations from normality. The distributions of the skinfold measurements, forearm length, calf circumference, bizygomatic

Table 1. Variables Included in the Principal Components Analysis

Head	Postcranial Skeleton	Additional Variables
Head Breadth	Cervical Height*	Stature
Head Height	Biacromial Diameter	Weight
Head Length	Transverse Chest	Log10 Triceps Skinfold
Bizygomatic Diam.	A-P Chest Diameter	Log10 Subscapular
Bigonial Diameter	Bi-iliocristal Diameter	Skinfold
Nose Breadth	Trunk Length*	Log10 Suprailiac
Nose Height	Upper Arm Length	Skinfold
	Log10 Forearm Length	Upper Arm Circumference
	Hand Length	(Relaxed)
	Bicondylar Humerus	Thigh Circumference
	Wrist Breadth	Chest Circumference
	Hand Breadth	
	Upper Leg Length*	
	Lower Leg Length	
	Foot Length	
	Bicondylar Femur	
	Ankle Breadth	

*Derived from variables on the IBP full list.

Cervical Height = Stature - Head Height - Suprasternal Height

Trunk Length = Suprasternal Height - Height Anterior Superior Iliac Spine

Hand Length = Total Arm Length - Upper Arm Length - Forearm Length

Upper Leg Length = Total Leg Length - Height Tibiale

     (Total Leg Length = Stature - Sitting Height)

diameter, face height, and cervical height differed significantly ($p<.05$) from the normal distribution. Logarithmic transformations (base 10) improved the distributions of the skinfold measurements and forearm length. These variables were then retained. Log10 transformations failed to improve the distributions of bizygomatic diameter, face height, and cervical height. Face height was dropped from the analysis. Bizygomatic diameter was retained without transformation in order to avoid further reduction of the number of head measurements available for analysis. The variable cervical height provided an additional segment of total body length for the analysis. For this reason, the untransformed variable was retained. The distribution of calf circumference could not be improved with a log transformation and the variable was dropped from the analysis. In the present study, the information provided by lip

thickness and mouth width was limited, so these variables were dropped in order to increase the degrees of freedom associated with the analysis.

Principal Components Analysis

Principal components analysis is a statistical technique which summarizes data by extracting components which are linear combinations of the measured variables. The objective of the method is to explain the variance in a data set (Kin and Mueller 1978). Principal components are extracted in the following manner. The axis of the first principal component is established within the region in multidimensional space which has the greatest variance within the data set. This axis is established by minimizing the squared deviations between the axis and the variable points. The axis of the second principal component is established within the region which has the second greatest variance, but is necessarily orthogonal to the first principal component. The process is continued with each principal component thereafter with the number of components equaling the number of variables in the analysis. The principal components are orthogonal to each other and thus independent. Although the number of principal components equals the number of variables in the analysis, a large percentage of the total variance is usually accounted for by a relatively small number of components. This is the objective of the method. Once the principal components have been extracted, they may be interpreted by examining the loadings or weights that each variable has received for each component. When the data have been standardized, the loadings may be interpreted as the correlation coefficient of the variable and the principal component. Following oblique rotation, the loadings may be interpreted as the partial correlation of the variable and the principal component, excluding the effect of the other principal components. An initial principal components solution usually consists of a general size component with positive loadings for most or all of the variables and a series of bipolar components which represent shape (Blackith and Reyment 1971).

Because the number of degrees of freedom associated with the principal components analysis was limited, the relevant statistical assumptions were carefully checked. A satisfactory principal components solution is dependent on two important assumptions: 1) the distribution of the variables must be multivariate normal and 2) when data from two or more groups which differ in some way are being combined, the covariance matrices of each must be similar so that they (or the correlation matrices) may reasonably be pooled. With a data set containing a large number of variables, multivariate normality is not usually a problem because fluctuations in the distributions of the individual variables which may be due to sampling

error are counterbalanced by the multivariate distribution as a whole. The primary danger here is from unusual observations, which can be difficult to identify. None have been observed in this data set. As in the univariate case, when the assumption of multivariate normality is violated, inferences about any group of unmeasured individuals are not appropriate. Johnson and Wichern (1982) suggest that when the corresponding elements of the sample covariance matrices differ by a magnitude of four or greater the consequences for the analysis may be serious. The within group covariance matrices for all 32 variables were compared and it was found that the rule was violated in a number of instances. The pooled covariance matrix may therefore be a poor estimate of the true population covariance matrix. This applies to the pooled correlation matrix as well.

If further clarity of interpretation is desired, an initial principal components solution may be rotated with either an orthogonal or an oblique method of rotation. Theoretically, in a factor analysis each observed variable will have a non-zero loading on only one factor. However, two characteristics of the common factor model may lead to non-zero loadings for variables on more than one factor. These characteristics are: 1) the requirement that factor axes be orthogonal and 2) the sequential extraction of factors in order of greatest to least variance explained. These comments apply to principal components analysis as well. Methods of rotation are designed to reduce the marginal non-zero factor loadings of each variable and thus obtain a solution with simple structure. Orthogonal or fixed axis methods of rotation retain the existing relationship between the axes of the principal components. Axes are positioned as close to the variable clusters as possible while maintaining orthogonality. In oblique rotation, the requirement of orthogonality is abandoned, and component axes are positioned within the variable clusters. In the absence of natural independence the principal components are then correlated. Kin and Mueller (1978) have discussed the reasons why factor rotation is often necessary and the theory behind orthogonal and oblique methods of rotation.

In order to obtain maximum clarity of interpretation, an oblique rotation was applied to the initial principal components solution. The resulting correlation of the principal components was considered in keeping with biological reality, because of the factors common to growth of the entire body. The method of choice was Promax (Hendrickson and White 1964). In the Promax method, the initial factor or component solution is first rotated to simple structure using an orthogonal technique, in this instance Varimax. The resulting solution then serves as the target matrix for the oblique rotation. The resulting oblique components are the best fit to the target matrix. This procedure is based on the assumption that the simple structure obtained by

the orthogonal rotation will be similar to that which would be obtained by an oblique rotation. The principal components are naturally independent or nearly so (Kin and Mueller 1978).

Discriminant Analysis

When the object is to explore group differences, as in this case between the Quechua and the Aymara, discriminant analysis is comparable to a significance test for differences in group means in the multivariate setting. In order to examine the discriminatory potential of each principal component, a stepwise selection procedure was performed using component scores as data. The component scores were computed using standardized scoring coefficients and the standardized raw data. At each point in a stepwise procedure, an additional variable is considered for entry into the model and all variables are considered for removal. The statistic used in examining the discriminatory potential of the principal components was Wilks' Lambda, which examines the differences between clusters of observations and the degree of cohesiveness within the clusters. This statistic is equivalent to a multivariate F statistic used in testing for differences in population means. In this stepwise procedure, partial F statistics were employed to determine both the entry and removal of variables from the model. The F-to-enter tests the statistical significance of the additional discriminatory power that a variable adds to the model. The F-to-remove tests the statistical significance of any loss in discriminatory power if a variable were to be removed from the model. The initial F-to-enter values indicate whether or not the discriminatory power of each variable is statistically significant. The initial F-to-enter values are equivalent to full multivariate F statistics computed for each variable separately.

The most important assumptions in the form of discriminant analysis used here are: 1) that the distributions of the discriminating variables be multivariate normal and 2) that the group covariance matrices be fairly similar so that they may be pooled reasonably. The distributions of the variables were plotted and a univariate test for normality performed for both the pooled and group samples. No statistically significant variations from normality were found in the distributions of the variables in the analysis. No outliers were identified. The hypothesis of equal covariance matrices may be tested by computing a likelihood ratio in which the product of the group matrix determinants is divided by the pooled matrix determinant (Kendall and Stuart 1961). The group covariance matrices in the analysis did not differ at the $p=.05$ level of significance. Klecka (1980) discussed stepwise discriminant analysis and the statistical assumptions required in discriminant analysis.

Statistical procedures were performed using SAS (SAS User's Guide, 1982) and the computation facilities of The Pennsylvania State University (IBM 360/370).

RESULTS

Presented below are: 1) the results of the whole body principal components analysis, in which a combined sample of Quechua and Aymara males was used, and 2) the results of the whole body discriminant analysis, in which the principal components were tested for group differences between Quechua and Aymara. The statistical assumption of equal group covariance matrices was not fully upheld in the whole body principal components analysis. As a result, the actual covariance relationships of the measured variables may not be expressed in the principal components solution.

Principal Components Analysis

The rotated principal components and accompanying descriptive data are presented in Table 2. The first seven principal components were retained. Each of these components accounted for five or more percent of the total variance in the data set. The final communality estimates are the sums of the squared component loadings of each variable. The final communality estimates represent the percentage of the variance of each variable that was explained by the seven principal components. The percentage of the total variance explained by each component following Varimax rotation showed how the variance was divided among the components when orthogonality was maintained. The orthogonal solution accounted for 66.67% of the total variance. The percentage of the variance explained by each principal component, eliminating other components, showed the unique contribution of each component following oblique rotation. The unique contributions of the oblique principal components accounted for 57.52% of the total variance.

The seven principal components are described and interpreted below. Loadings of 0.4 or greater were considered in the interpretation of the principal components. The value of 0.4 was arbitrary.

Principal Component 1. The highest loadings were found for major dimensions of the body, including measures of chest size, and circumferences of the upper arm and thigh. The component was interpreted as *general body form* or bulk, containing elements of bone and soft tissues. Body weight was included in this component as well.

Table 2. Rotated Principle Components and Accompanying Descriptive Data

Principle Component	Variable	Component Loading	% Total Variance (eliminating other components)	Cumulative % Total Variance
1 General Body Form	Chest Circumference	.82	10.90	10.90
	A-P Chest	.70		
	Upper Arm Circ.-rel.	.64		
	Transverse Chest	.59		
	Weight	.55		
	Thigh Circumference	.43		
	Bicondylar Humerus	.41		
2 Form of the Skeletal Framework	Stature	.70	9.50	20.40
	Bi-iliocristal Diam.	.68		
	Cervical Height	.68		
	Upper Arm Length	.66		
	Upper Leg Length	.57		
	Log10 Forearm Length	.51		
	Biacromial Diameter	.45		
3 Fatness	Log10 Subscap. Skinf.	.85	9.55	29.95
	Log10 Triceps Skinf.	.84		
	Log10 Suprail. Skinf.	.83		
	Thigh Circumference	.44		
	Trunk Length	.42		
4 Robustness of Extremities	Ankle Breadth	.85	7.76	37.71
	Wrist Breadth	.59		
	Hand Breadth	.58		
	Foot Length	.47		
	Nose Height	.44		
5 Uninterpreted	Head Height	.75	7.26	44.97
	Bicondylar Femur	.75		
	Nose Height	-.59		
	Bicondylar Humerus	-.49		
6 Cranial Breadth	Nose Breadth	.69	6.51	51.48
	Head Breadth	.62		
	Hand Length	-.57		
	Biacromial Diameter	-.56		
7 Skull Breadth	Bizygomatic Diam.	.89	6.04	57.52
	Bigonial Diameter	.61		

Principal Component 2. Major lengths and breadths of the skeletal framework had high loadings. The component was interpreted as representing *form of the skeletal framework*.

The first two principal components represent general body form and body linearity, respectively. When anthropometric data are analyzed, unrotated factor analytic solutions usually have as the first factor one representing general body size, with high positive loadings on all major dimensions of the trunk, limbs, stature, and weight (Burt and Banks 1947, Hammond 1957, Masuda 1965, Vandenberg 1968, Kouchi 1979). Following rotation this general size factor may be divided into two factors, the first characterized by major body breadths, circumferences, and weight, and the second characterized by stature and other longitudinal measurements of the body (Burt and Banks 1947, Vandenberg 1968). This was the case in the present analysis, although there was some mixing of breadth measurements with high loadings for bi-iliocristal diameter and biacromial diameter in the second principal component. The second factor of Howells (1951) was also characterized by longitudinal measurements of the body plus bi-iliac breadth.

Principal Component 3. This component had high loadings for the three skinfolds and marginal loadings for thigh circumference and trunk length. The component was interpreted as one of *fatness*. Factors and principal components characterized by skinfold measurements or body circumferences have been identified in a number of studies (McCloy 1940, Howells 1951, Hammond 1957, Relethford et al. 1978).

Principal Component 4. This component consisted of lengths and breadths of the distal portions of the extremities plus nose height. The component may actually represent breadth of the extremities. Hand breadth had a fairly high loading while that of hand length was approximately zero. The moderate loading of foot length may have been due to the fact that there was no measure of foot breadth in the analysis. The component was interpreted as representing *robustness of the extremities.* This was primarily a skeletal component. Nose height and several cranial variables with loadings of less than 0.4 were considered extraneous to the component. Similar factors and principal components have been identified in other studies (Hammond 1957, Vandenberg 1968, Kouchi 1979).

Principal Component 5. This component could not be clearly interpreted. It appeared to consist of two opposing pairs. Such an opposition as between head height and nose height, has been found in other factor analytic studies (Howells 1951). In the present study bicondylar femur and bicondylar humerus are opposed but the cause for such opposition was not at all clear. Because the bipolarity of the component remained following rotation, the opposition of the two extremity widths may have been an artifact of the computations rather than a biologically meaningful result. A similar situation arose with principal component 6, which also retained a bipolar structure following rotation.

Principal Component 6. The interpretation of this component was also unclear. Head breadth and nose breadth were opposed by biacromial diameter and hand length. Such a combination of head measurements has not been found in any factor analytic study known to this author, although measurements of the nose sometimes associate with other facial measurements and with measurements of the calvarium (Relethford et al. 1978). This combination of postcranial measurements appears to have no readily evident biological meaning. It may be that the strong negative loadings of the postcranial variables were present simply to balance the strong positive loadings of the head variables. This situation sometimes occurs in the initial solution of factor and component analysis but usually disappears after rotation (Howells 1951, Hammond 1957). The component was interpreted as one of *cranial breadth*.

Principal Component 7. This component had high loadings for bizygomatic diameter and bigonial diameter. It was associated primarily with the face, but had a loading for head breath of 0.39. Thus, the component was interpreted as one of *skull breadth*. Because precise comparability of measurements is lacking, it is difficult to compare head factors identified in different studies. Howells (1951) identified a factor (which he designated V 14) with the same constituents as principal component 7 in this study, but associated with them were other measurements of head breadth as well. Relethford et al. (1978) identified a head breadth component (his PC 3) with the same constituents as principal component 7 in this study, but with one additional measure of head breadth. Relethford et al. suggested that this component could be identified with cranial robustness. Landauer (1962) identified two factors (designated in his study as V 3 and V 21) related to width in the malar region; one was associated with size and the other with robustness.

The correlations among the principal components identified above were rather low, indicating that the orthogonal factor model approximated biological reality in this instance. All 32 measured variables regardless of loading, were included for each principal component in the computation of the partial correlations.

Table 3 shows the partial correlations of the principal components. None of the partial correlations had an absolute value greater than 0.29, and many were negligible. Most of the strong partial correlations were with principal component 1. This was not surprising because component 1 was a general component with high positive loadings for approximately one-third

Table 3. Partial Correlations of the Principal Components
Following Oblique Rotation

	1	2	3	4	5	6	7
1	1.00						
2	0.29	1.00					
3	0.02	0.05	1.00				
4	0.20	0.11	0.09	1.00			
5	- 0.09	-0.06	-0.04	-0.03	1		
6	- 0.12	-0.05	-0.03	0.08	0.29	1.00	
7	0.22	0.18	0.00	-0.16	-0.1	-0.09	1.00

of the variables in the data set, particularly those which combine the skeleton and the soft tissues. With the exception of principal component 6 (cranial breadth), the components based primarily on skeletal measures (principal components 2, 4, 7) were positively correlated with component 1. Principal component 3, the fatness component, had negligible partial correlations with all other components. The partial correlations between the head components (principal components 6 and 7) were negligible. Partial correlations of the head components with those of the trunk and limbs ranged between -0.16 and +0.22. A comparison of the unique contributions of the components following oblique rotation with the percentage of the total variance explained by each component in the orthogonal solution also indicated a low degree of intercorrelation among the components (Table 3). From a total of 66.67% of the total variance accounted for in the orthogonal solution, only 9.15% was shared among the oblique principal components. Of this discrepancy, 4.02% was attributed to principal component 1. These findings indicated that it was legitimate to perform separate significance tests for group differences between each of the oblique principal components.

Discriminant Analysis

The results of the stepwise discriminant analysis on the principal components described above are shown in Table 4. The Aymara had the higher mean component scores for all principal components. Principal component 5 was excluded from the discriminant analysis because it could not be clearly interpreted. Furthermore, only those variables considered in the interpretation of the principal components were included in the discriminant analysis. The scoring coefficients of all other variables were set to zero. Additional exclusions were made as noted below. The probabilities shown were those associated with the initial F-to-enter values computed by the stepwise procedure. For the fatness component, differences between Quechua

Table 4. Discriminant Analysis of Principal Components for Group
Differences Between Quechua and Aymara

Principal Components		p Value	Group with Greater Mean Value
Number	Designation		
1	General Body Form	0.2720	Aymara
2	Form of the Skeletal Framework	0.5364	Aymara
3	Fatness	0.0011*	Aymara
4	Robustness of the Extremities	0.1079**	Aymara
6	Cranial Breadth	0.0149	Aymara
7	Skull Breadth	0.0392	Aymara

*Trunk length was excluded from the analysis.

**Nose height was excluded from the analysis

and Aymara were highly significant ($p<.0011$) with the Aymara reflecting the effects of greater skinfold measurements. Trunk length was not included in the discriminant analysis of this component because the biological relationship between this variable and body fatness is unclear. Statistically significant group differences were also found for both head components ($p<.04$), with the Aymara having a broader craniofacial complex than the Quechua. Group differences in robustness of the extremities approached statistical significance ($p <.1079$), with the Aymara having broader extremities than the Quechua. Nose height was not included in the discriminant analysis of this component because in factor analytic studies, craniofacial dimensions generally do not mix with postcranial dimensions, except in general size factors (Howells 1951, Relethford et al. 1978). Nose height might well be considered extraneous in a principal component with high loadings on dimensions of the extremities. The results of the discriminant analysis did not suggest any clear cut group differences in general body form or form of the skeletal framework.

With the significance levels for entry and removal of variables from the model both set at 0.01, the stepwise procedure added no additional variables to the model after the fatness component was entered. The cranial breadth component was added to the model in addition to the fatness component. Thus the skull breadth component did not add any discriminatory power to the model once the fatness and cranial breadth components were entered.

The results of the principal components analysis were similar to those of other factor analytic studies, suggesting that the sample covariance matrix was a fairly good estimate of the population covariance matrix.

DISCUSSION AND CONCLUSIONS

The principal components analysis on the Quechua and Aymara population studies yielded components similar to other factor analytic studies using anthropometric data. Principal components 1 and 2 are shape components, with principal component 1 containing major body circumferences and breadths, and principal component 2 containing major body lengths and breadths. The first component has a large contribution from the soft tissues, while the second is primarily skeletal. The results of the discriminant analysis indicate that, as judged from these relatively small samples, Quechua and Aymara do not clearly differ in overall body shape. The mixing of length and breadth measurements in principal component 2 differs from some factor analytic studies (Burt and Banks 1947, Vandenberg 1968) and may be the result of random fluctuations in the measured variables due to small sample size. This mixing of disparate elements limits the usefulness of the principal components because a more general interpretation of the results is required.

These Quechua and Aymara groups do differ in more specific morphological characteristics, i.e. the Aymara are fatter and have a broader craniofacial complex than the Quechua. Earlier studies have also found Aymara groups with larger anthropometric dimensions than the Quechua groups with which they were compared. Stinson (1980) compared the growth of Aymara children from Ancoraimes, Bolivia, with Quechua children from Nuñoa, Peru. After age fifteen, Aymara males from Ancoraimes were taller, heavier, and fatter than the Quechua males from Nuñoa. Adult male Aymara from the Chilean altiplano, studied by Mueller et al. (1980), were taller and heavier than adult male Quechua from Coata (Eckhardt et al. 1982). The findings of the present study and those of Eckhardt et al. (1982,1983) indicate that physical differences between Quechua and Aymara may exist even when the groups compared are living at the same altitude under the same climatic conditions.

Although the anthropometric differences between Quechua and Aymara appear to be consistent, the sources of these variations are unknown. Mueller et al. (1980) provide evidence for the plasticity of head shape in native Andean highlanders. Statistically significant differences were found in head breadth, head length, and bizygomatic breadth between adult male Aymara from the Bolivian altiplano and adult male Aymara from the Chilean altiplano. No statistically significant differences in these dimensions were found between the adult females of this group. In postcranial dimensions, statistically significant differences were found in sitting height and sternal length between adult females of the Bolivian and Chilean Aymara groups while the adult males did not differ significantly in these dimensions.

Similarly, the adult males of the two Aymara groups had significantly different anterior-posterior chest dimensions, while the adult females did not. Thus the differences in head shape and postcranial morphology between the Quechua and Aymara groups in the present study may not be of biological significance.

Discriminant analysis of principal components may reveal group differences in gross body morphology. It has been clearly demonstrated that the Camacani Aymara are fatter and have a broader craniofacial complex than the Coata Quechua. These differences, suggested by the univariate comparisons performed by Eckhardt et al. (1982,1983), are confirmed here. The univariate comparisons also suggested a more general difference in body breadth between these groups, with the Aymara having broader trunks as well as longer limbs. This potential group difference is not confirmed. This points out a limitation of the approach taken in this analysis. Important relationships may not be expressed by the principal components solution. Due to the mathematical characteristics of the common factor model, a principal component may contain variables whose biological relationship to the other variables in the component is not particularly meaningful. Thus the results of significance tests may be confounded. This problem can be alleviated to a certain degree by performing principal components analyses on separate functional complexes of the body.

Several studies have found differences in skeletal and soft tissue morphology between the Quechua and the Aymara, with the Aymara being the physically larger group in each case. This suggests a common source for the observed variation between Quechua and Aymara. If this is the case, the close biological and cultural relationship of these two groups affords a special opportunity to explore the potential sources of genetic variation between human populations.

CHAPTER 5

HERITABILITY ESTIMATES OF SIX ANTHROPOMETRIC INDICATORS OF NUTRITIONAL STATUS IN A HIGH ALTITUDE PERUVIAN POPULATION

George Joseph Vandemark

ABSTRACT

Human populations native to high altitude in the Andes are characterized by a complex of distinctive morphological features which distinguish them from sea level inhabitants of comparable sexes and ages. One of the most obvious features is the reduced body weight of high-altitude natives relative to their sea level counterparts. The nature of this adaptation is uncertain. Some studies indicate that this difference is the result of developmental changes that take place within the lifespan of an individual in response to environmental stresses. Other studies suggest that the reduced weight might in part result from inherited genetic mechanisms shaped by natural selection. Selection cannot produce changes in the population mean of a quantitative trait unless additive genetic variation is present. The objective of this paper is to estimate the amount of additive genetic variance present in six traits which define the nutritional status in the study population.

Data for this analysis comprise measurements of body weight, upper arm circumference, and skinfolds taken on a Peruvian population residing in Camacani, Peru, at an altitude of 3900 meters above sea level. The observed measurements were transformed to age and sex specific z-scores and heritability estimates were derived by the methods of mother-offspring regression, father-offspring regression, midparent-offspring regression, and full sib analysis of variance.

Body weight and upper arm circumference are the two traits that best define nutritional status. These two traits had moderate heritability estimates. These two traits also showed evidence of substantial maternal effects. The results of this study indicate that there is sufficient additive genetic variation on which natural selection could act to influence the body weight and nutritional status of this high-altitude population.

INTRODUCTION

Environment of Highland Peru

In Peru, the average altitude of the Andes is 4880 meters, and the highest elevation is 6550 meters (Jenks 1956). The formation of these mountains began approximately five million years ago with uplift during the Pliocene and Pleistocene (Jenks 1956). The relative youth of this mountain range results in rugged topography and immature soil. The cold and dry environment inhibits the decomposition of organic matter, resulting in slow soil evolution. Solifluction, the downward movement of surface materials due to the freeze-thaw cycle, also inhibits soil development (Thomas and Winterhalder 1976).

The human population under examination in this study resides in an area collectively referred to as the altiplano (Pearson 1951), that treeless portion of the central Andes surrounding Lake Titicaca. The climate of the altiplano is affected by its physical position on the earth, circulation patterns of air and water masses, and surface features.

The following description of the Andean altiplano climate relies on material provided by Eidt (1968). Precipitation is seasonal in the altiplano. Rainfall begins in September, reaches a peak intensity in January, and ends in April. Moist air from the South Atlantic anticyclone is blown west and releases its moisture on the eastern side of the Andes. The barometric pressure and temperature of this air increases as it moves down the westward slope of the Andes. This process causes an increased capacity to hold water and this air mass desiccates the altiplano by evaporating moisture from vegetation and soil. Consequently, droughts of up to one year are common in the altiplano. Droughts involving irregular monthly precipitation distributions can be equally devastating if they occur during September or October, the beginning of the planting season. The altiplano has a generally constant mean temperature because of its location within the earth's tropical region. During the period from 1931 to 1972, the monthly mean maximum temperature was 17.3°C and the monthly mean minimum was -3.0°C, giving a range of 20.7°C (Thomas 1976). However, because of the lack of vegetation and thin atmosphere associated with high altitude, the altiplano exhibits extreme diurnal temperature variation. The daily high of approximately 17°C occurs in the afternoon and on clear nights the temperature may plunge below freezing. This diurnal variation results in the possibility of frost occurring during any time of the year.

In all, the altiplano is a difficult environment for human habitation. Thomas (1976) considered the following potential stresses of the Peruvian highland environment that will be summarized here. The first is the reduced partial pressure of oxygen as a function of altitude. The rugged topography and poorly developed soil also adversely affect human inhabitation.

Another stress associated with the Peruvian highland environment is the pronounced diurnal variation in temperature and intense frosts. Finally, the irregular monthly precipitation distribution can be considered a stress; droughts are unpredictable in the altiplano and can last several years.

Any organism must make adaptive morphological and physiological changes to survive in this harsh environment and *Homo sapiens* is no exception to this rule. The following section will detail growth patterns of the native high-altitude Peruvian which are distinct from those of his sea level counterpart.

Growth Patterns of High-Altitude Peruvians

High-altitude adults are shorter than Peruvians of predominantly European ancestry. Hurtado (1932a) found the average height for Quechua Indians was 159 cm compared to an average of 168 cm for Peruvians of European ancestry. The high-altitude growth period is slow and prolonged, continuing until the twenty-second year (Frisancho 1976). The regression of stature on age reveals approximately equal growth rates for males and females (Greulich and Pyle 1959). The continuing social improvement of modern society relative to the stasis of the subsistence economy of the Peruvian highlands could continue to increase the difference in stature between highland and sea level inhabitants.

The total body weight of high-altitude Peruvians is less than that of their sea level counterparts. The weight of rural highland Quechua Indians is also less than that of urban lowland Quechuas (Frisancho and Baker 1970). Lowland Quechuas also have 20% more fat than high-altitude Quechuas (Frisancho and Baker 1970). This discrepancy may be due to a greater calorie surplus in low-altitude Quechuas. This difference may also be attributable to different levels of physical activity between the low and high altitude Quechua populations.

Sexual maturation and dimorphism are delayed in high-altitude Peruvians. Clear sexual differences in fat deposition occur in Peruvian highlanders at the age of 14 years, while in U.S. samples, the difference is evident by the age of eight years (Baker et al. 1958). Sexual dimorphism in regard to muscle development is not evident until 18 years in highland Peru while it is evident in U.S. samples before age 14 years (Baker et al. 1958). Menarche occurs later in high-altitude girls than among sea-level girls of the same socioeconomic and nutritional status. The studies of Donayre (1966) demonstrated a mean age at menarche of 11.58 years in sea level girls while at 3000 m the average age at menarche was 13.58 years. Data of Llerena (1973) indicate that females reach adult levels of luteinizing hormone by the age of 11 years at sea level and 12 years at an altitude of 2500 m. Differences between high and low

altitude inhabitants are also observed in the sexual development of males. A sample of males with an age range of 7 to 15 years revealed that 76% of high-altitude boys were in the prepubertal stage while only 39% of the sea level boys were prepubertal (Llerena 1973). The studies of Guerra-Garcia (1971) demonstrated that the excretion of urinary testosterone is lower in adults at high altitude than at sea level.

It should be realized that these distinctive growth patterns of high-altitude natives are the result of interaction between genetic and environmental influences. Some of these environmental influences include nutrition, hypoxia, and cold temperatures. The relative influence of these and other factors on the expression of genetic potential produces the phenotype of the individual. The following section will describe the nutritional status and diet of Peruvians inhabiting the altiplano in an attempt to define more clearly the interaction between genotype and environment.

The Andean Diet

The Peruvian Andes can be divided into two major ecological zones. The sierra consists of lands from sea level to 3200 m (Picón-Reátegui 1976). The cultivation of cereals, tubers, sugar cane, bananas, and other crops is possible within this range of altitudes. The resultant dietary diversity may be a principal cause of the long history of dense habitation of the Peruvian sierra.

The second zone, the puna, can be classified into two subzones: the jalca, which begins at 3200 m, and the true puna, which begins at approximately 3800 m (Picón-Reátegui 1976). Natural pasture grows in the jalca but the true puna is characterized by poor soil and cold temperatures which inhibit agricultural success. Only potatoes and species of the genus *Chenopodia*, such as quinoa, can grow successfully in the true puna (Picón-Reátegui 1976). Because of the lack of roads, dietary habits have been closely linked to local food sources for generations.

The most substantial quantitative analysis of the high-altitude Peruvian diet was conducted by Gursky (1969) in the town of Nuñoa, which lies at an altitude of 4000 m. The data indicate that the typical native diet obtained 86% of the total caloric intake from carbohydrates, 8.1% from proteins, and 5.6% from fats. Vegetable products accounted for 93.7% of the total mass of the diet, of which over 80% was either potatoes or quinoa. These values can be taken only as gross estimates because there is some seasonal variation in the diet associated with harvesting cycles.

No quantitative analysis of diet has been conducted in the town of Camacani, from which the sample population for this study was derived. Certain environmental factors indicate that the average nutritional level in this town exceeds that in Nuñoa. Dietary staples in both towns include potatoes and quinoa, but the proximity of Camacani to Lake Titicaca makes the exploitation of animal food sources easier than in Nuñoa. Camacani residents can supplement their diet with fish from the lake, and the reeds bordering the shore can be used as food for livestock. It is probable that the inhabitants of Camacani consume more animal products per capita than the inhabitants of Nuñoa, including more fat as well as more protein.

The apparently greater nutritional adequacy of the Camacani diet relative to the Nuñoa diet may be responsible for the observation that the average Camacani male weighs 5 kg more than his Nuñoa counterpart (Eckhardt and Dutt 1979). Varying levels of physical activity between the two populations probably cannot account for this observed difference in body weight because males of both populations spend approximately 12 to 14 hours a day engaged in pastoral or agricultural labor (Picón-Reátegui 1976).

Objectives

The previous sections indicate that there are numerous adaptations established by the Andean natives in response to high altitude. The developmental basis of this adaptive complex is still uncertain. The objective of this study is to assess, for one Andean community, the amount of additive genetic variance present in traits which reflect nutritional status. The traits studied comprise body weight, upper arm circumference, subscapular skinfold, suprailiac skinfold, mid-axillary skinfold, and triceps skinfold.

REVIEW OF PREVIOUS STUDIES

The mechanisms which govern the morphological development of high-altitude Peruvian populations are not well understood. Certain evidence indicates that continued habitation of such a harsh environment for thousands of years could result in natural selection operating on the population. This would result in a genetic component being present in the differences between Peruvian populations. Other evidence supports the view that differences between low and high altitude natives are due to developmental changes. These changes are thought to occur within the individual's life span in response to specific environmental

influences. Previous studies concerning both views will be reviewed in the following two sections.

Studies Suggesting a Developmental Causation

The position that the morphological differences between low and high altitude Peruvians are due to developmental changes within an individual's life span, in response to environmental stresses, is supported by the evidence of Frisancho (1969, 1975). Frisancho (1975) compared low and high altitude Quechua populations of the same ethnic background. The subjects had resided in their respective environments for at least one generation. The highland natives, in general, had larger maximal chest circumferences. These two populations had similar ABO and Rh blood group systems so Frisancho concluded that the populations were genetically similar and that differences between the two populations were due to environmental effects. However, it is possible that loci controlling chest development are under different selective pressure in both environments. The resultant changes in the frequencies of genes controlling chest morphology could be responsible for the differences between the two populations.

Many laboratory results indicate that once selective pressures are removed, the phenotypic response of the population is in the direction opposite to that of selection (Falconer 1960). The lowland population studied by Frisancho did not consist of first generation offspring of high-altitude natives; therefore, it is possible that at least one generation of reverse selection may have operated in the lowland population.

A study by Lahiri et al. (1976) concerning the diminished response to hypoxia characteristic of high-altitude natives also advocated an environmental influence on the development of a phenotype characteristic of high-altitude natives. The presence or absence of hyperventilation under simulated hypoxic conditions was examined. Young migrants (less than 12 years old) from high to low altitude showed a normal ventilatory response whereas older migrants (over 15 years old) exhibited the diminished ventilatory response characteristic of high-altitude natives. These findings indicated that the adaptation to a hypoxic environment was related to the amount of time spent at high altitude. However, Lahiri had a very small sample size: 58 high-altitude children (13 to 20 years), and 40 high-altitude adults. He also neglected the observation that no migrants from low to high altitude exhibited a diminished ventilatory response.

In certain environments, the stress of high altitude hypoxia on absolute stature and growth rate may be counterbalanced by a reduced incidence of disease. In Ethiopia, the growth

patterns of genetically similar lowland and highland populations were analyzed (Clegg et al. 1972). The highland population grew taller and faster than the population in the more disease-prone lowlands.

We should expect the body weight of high altitude Peruvians to be under the influence of two major environmental stresses associated with high altitude: cold and hypoxia. It appears that the influences of these two stresses on body weight are in opposite directions. Acute exposure to hypoxia is associated with large losses of body weight over days or even weeks (Consolazio et al. 1968). This includes both water and tissue loss. However, initial exposure to high altitude is also characterized by hypohydration and anorexia. The extent to which the observed weight loss is due to hypoxia is uncertain in light of these other two factors. It should be noted that this observation is the proximate result of short term exposure to high altitude. The ultimate result of high-altitude residence for many generations on body weight is uncertain.

Cold temperatures tend to increase body weight relative to the amount of skin surface in order to insulate against heat loss. Roberts (1953) observed indigenous peoples from different geographical locations and calculated that the average human male gains 0.305 kg for every one degree Fahrenheit fall in mean annual temperature. An environmental influence on body weight is supported by the studies of Newman and Munro (1955), who sampled a large population of North American males of European ancestry. If the hot-cold weight clines were the result of natural selection then they should not be observed in this sample of recent migrants from Europe. The study demonstrated a high positive correlation between body weight and annual temperature. Although this study does not disprove that the cline is due to genetic influences, it does suggest that most of the variation in weight is due to environmental factors.

The most obvious environmental influence on weight and growth rate is an individual's diet. Frisancho et al. (1970) found that lower class Central American adolescents had a 30% reduction in structural growth and a 10% reduction in skeletal maturation compared to U.S. standards. Malhotra (1966) demonstrated that Indian Air Force recruits from southern India, the most nutritionally deficient part of the country, gained more weight than recruits from the more nutritionally adequate central and northern regions when all the recruits were fed the same diet.

Studies have indicated that another environmental influence on body weight is overnutrition. Financially secure New York mothers had newborn and stillborn infants with more subcutaneous fat and larger adipose cells than those of poorer mothers (Naeye et al. 1971). The results concerning socioeconomic status and adult weight are conflicting. A Manhattan

study found that 30% of lower class women were obese, 16% of middle class women were obese, and 5% of upper class women were obese (Stunkard 1968). Among Manhattan males studied, 32% of the lower class and 16% of the upper class were considered obese. However, in Germany the greatest obesity was observed in upper class males and lower class females (Newman 1975). The German males appear to have a caloric surplus for the sedentary life style of upper class males while the weight of lower class females is probably the result of a high carbohydrate, high fat, and low protein diet which is characteristic of many lower socioeconomic groups (Newman 1975).

Physical activity is an environmental factor influencing the amount of adipose tissue in mammals. Endurance running initiated early in life (pre-weaning) reduced the rate of fat cell accumulation in rats, and subsequently resulted in reduced amounts of body fat later in life (Oscai et al. 1974). Running initiated after seven weeks did not reduce adipose cell number but reduced adipose cell size (Askew and Heckler 1976). It appears that the pattern of fat cell proliferation is established by the age of seven weeks in rats. Studies on human infants indicate that adipose cells multiply when the cells are filled with lipid to a size comparable to that of young adults (Hager et al. 1976). Since physical activity can reduce cell size, and in light of a suggested correlation between size and cell division, a reduced cell size may delay or inhibit adipose cell proliferation.

Physical activity is an important factor in the maintenance and regulation of body weight. Weight is a heterogeneous measurement that can be partitioned into lean body mass and fat (Malina 1969). Regular physical activity in children and adolescents produces an increase in lean muscle mass and a corresponding decrease in fat (Parizkova 1973). Training produces the same effect in adults, usually with no change in body weight (Parizkova 1963).

Family size may also be an environmental factor influencing body weight. A twenty-three year longitudinal study of 9006 Danish births examined different sized families (Mednick et al. 1984). Children from larger families weighed significantly less at ages 7 and 11 than children from smaller families.

Studies Suggesting a Genetic Causation

If the morphological development characteristic of the highland Peruvian is the result of adaptive genetic changes within the population, then two criteria must have been met: natural selection must have occurred, and there must have been a sufficient time interval for natural selection to have acted. The most pervasive selective pressure at high altitude is the reduced partial pressure of oxygen in the ambient air. The atmospheric pressure at 3000 m is 520

mm Hg as compared to 760 mm Hg at sea level. This reduces the amount of oxygen per unit volume of air and causes an oxygen deficiency in tissue and in the blood. Evidence implying the presence of natural selection can be seen by analyzing the partial pressure gradient from inspired air to the tissues. Andean natives have a smaller oxygen cascade than sea level natives, corresponding to the initially lower partial pressure observed at high altitude (Heath and Williams 1977). The process of oxygen transport requires the interaction of many gene products and is presumably under some degree of genetic influence. Garruto and Hoff (1976) discovered that the mortality component (I_m) of Crow's Index of Opportunity for Selection (I) was much larger than the fertility component (I_f) for a high-altitude Quechua population. The values of I_m and I_f were, respectively, 0.522 and 0.305.

Archaeological studies by MacNeish (1971) have examined a series of remains in the Ayacucho Valley of central Peru. These remains document continuous habitation of the region from 20,000 B.C.E. to the present. This represents about 1100 generations, sufficient time for selection to have occurred in the presence of even mild selection intensity.

Many studies have revealed a genetic component in the morphological development of high-altitude Peruvians. Naeye (1966) demonstrated that growth retardation in mice under hypoxic conditions was due to a low number of cells, while growth retardation associated with nutritional deficiency is due to a low mass of cytoplasm in individual cells. This indicates that the number of mitotic divisions has an influence on growth retardation associated with hypoxia. Hoff (1974) compared five chest measurements between lowland and highland inhabitants. In his study the low-altitude subjects were first generation offspring of migrants from high altitude. Except for chest depth in adolescents, no other chest measurement showed any statistically significant deviation in adults or adolescents. Since the parents of both the highland and lowland subjects were high-altitude natives, this implies that the similarities in chest dimensions, despite different environments, were due to inherited mechanisms.

A later study by Eckhardt and Dutt (1979) analyzed the proportion of genetic variation in twelve parameters that defined the Andean thoracic morphology. Midparent-offspring, father-offspring, and mother-offspring regressions were calculated from data collected on 845 native highlanders in order to obtain heritability estimates for the parameters (Kramer 1980, and this volume). Falconer (1960) demonstrated that traits closely associated with reproductive success have low heritabilities. However, care must be taken in making an assessment about a parameter's role in the reproductive success of an organism, based on its heritability estimate. This is because a low heritability estimate can result from the presence of a large component of environmental variance. The midparent-offspring heritability estimate

for sternal length in this high-altitude Peruvian population was 0.343 (Kramer 1980, and this volume). The heritability estimate for sternal length in a sea level Belgian population was 0.787 (Susanne 1977). The depth of the Andean chest was analyzed by the parameter anterior-posterior diameter of the thorax. A midparent-offspring heritability estimate of 0.280 was derived for anterior-posterior diameter of the thorax in this high-altitude Peruvian population (Kramer 1980, this volume). Clearly, a longer and deeper chest could be of selective advantage in the hypoxic Andean environment. It should be noted that only those traits directly associated with the thoracic complex showed low heritability estimates. The midparent-offspring heritability estimate of stature in this high-altitude population was 0.509 (Kramer 1980, this volume). Roberts et al. (1978) calculated a heritability estimate of 0.65 for stature in a West African population. These two values fall within the same range when the standard errors of the heritability estimates are taken into account.

The study of Llerena (1973) revealed that high-altitude girls attained adult levels of luteinizing hormone later than sea level girls. Studies in molecular biology indicate a genetic causation for this observation. Human luteinizing hormone (hLH) is a dimeric protein with two dissimilar subunits (Pierce and Parsons 1981). The alpha subunit of hLH is exactly homologous with the alpha subunit of human chorionic gonadotropin (hCG), while the beta subunits of hCG and hLH are dissimilar (Pierce and Parsons 1981). The beta subunit of hLH is coded by one gene while the beta subunit of hCG is coded by seven genes (Talmadge et al. 1983). This conclusion was the result of restriction enzyme analysis and differential hybridization patterns between human placental DNA and a cDNA probe for the beta subunit of hCG. Subclones were constructed for each of the seven beta subunit hCG genes and the beta subunit of hLH gene. Restriction enzyme analysis of these subclones indicates that the beta subunit hLH gene is linked to at least three of the beta subunit hCG genes (Boorstein et al. 1982). Chorionic gonadotropin is made by the first-trimester placental cells to stimulate steroid synthesis in the corpus luteum, whereas luteinizing hormone is produced in the pituitary at the onset of puberty (Pierce and Parsons 1981). The proper transcription of the gene for the beta subunit of hLH without the transcription of the adjacent genes for the beta subunit of hCG requires a sophisticated genetic regulatory mechanism. The exact nature of this mechanism will remain uncertain until further research in eukaryote gene expression is complete. This finding indicates that the discrepancies between low and high altitude girls in the attainment of adult levels of luteinizing hormone may be the result of temporal differences in the transcription of the genes coding for the two subunits of hLH.

Long term nutritional trends appear to produce evolutionary changes in *Homo sapiens*. Based on evidence from the variety and volume of animal bones found in *Homo erectus* living sites in Europe, it was concluded that the Pleistocene diet contained more animal than vegetable matter (Butzer 1971). Lederberg (1969) observed that protein malnutrition is a disease peculiar to humans only, and concluded that our species lost the genes responsible for the synthesis of the eight essential amino acids because of their ready availability in animal protein. According to Meggers (1972), the proportion of animal foods in the Meso-American diet has shrunk from 70% to 5% in only 9000 years. This is due to the encroachment on hunting grounds by an expanding population, coupled with the domestication of livestock and plants (Meggers 1972). Protein derived from vegetable matter has an adequate amino acid composition but is not easily digested by humans (Dubos 1965). It appears that 9000 years has not been enough time for humans to cope adequately with this extreme dietary change.

Nutritional studies indicate that causes of the slow rate of growth in stature and weight of high-altitude Peruvians are not adequately understood. The effects of a four-year school lunch program on young (7 to 12.9 years) and adolescent (13 to 17.9 years) males of a high-altitude Peruvian town were analyzed by Newman (1975). Young boys showed little significant increase in weight, upper arm circumference, or nine other physical parameters when compared to the increases in older boys. The cause of this incomplete improvement in the young boys is uncertain; it may be the result of genetic mechanisms, propagated by natural selection, which restrict early growth potentials. However, young boys are the most underpriviledged of all age and sex classes in the Peruvian highlands; they receive less food than other members of the family and insufficient clothing for the ambient temperature. They also may not be able to procure supplementary food outside the home as well as the older boys (Newman 1975). This socioeconomic effect may account for some of the discrepancies observed between older and younger boys.

Only a few studies have been conducted in order to obtain heritability estimates for body weight and skinfold measurements. Susanne (1977) analyzed variation in body weight and upper arm circumference in a sea level Belgian population. The sample consisted of 125 families, each of which contained both parents and two or three children. Measurements were converted to age and sex specific z-scores in order to account for differences associated with these factors. The midparent-offspring heritability estimate for weight was 0.625, and that for upper arm circumference was 0.458; no standard errors of the estimates were reported (Susanne 1977).

Devi and Reddi (1983) calculated the heritability estimate for body weight in a Jalari population of India. The Jalaris are a poor Hindu caste. A sample of 436 families was analyzed; each family consisted of both parents and at least two children. The resulting heritability estimate for body weight was 0.541 (Devi and Reddi 1983). No standard error of the heritability estimate was published.

Some human studies have utilized twin analyses to calculate heritability estimates. This is done by comparing the variation in a characteristic in monozygous twins with the variation in the same characteristic in dizygous twins (Klissouras 1984). Clark (1955) computed a heritability estimate of 0.69 for body weight in a Michigan population. His sample consisted of 23 male and 21 female monozygous pairs and 23 female and 14 male like-sexed dizygous twins. Twins were classified as dizygous if they were discordant in either the ABO, MN, or Rh blood group systems (Clark 1955). Klissouras (1984) estimated the heritability of body weight in a sea-level Greek population to be 0.80. The sample consisted of 39 pairs of twins (23 monozygous and 16 dizygous) of both sexes. No standard errors of the heritability estimates were published in either the study of Clark (1955) or Klissouras (1984).

In making inferences from these studies, certain problems inherent in twin analysis should be considered. First, twins share a common environment *in utero*. The between-pair variance contains components of variance due to genetics and a component due to common environment. Second, the object of heritability analysis is to estimate parameters of the population; twins are a small sample of most populations and the resulting standard errors of the estimates may be large. Furthermore, in order to estimate a population parameter, the environmental components of variance in twins must be the same as that of singletons. This may not be the case because monozygous twins are of three types depending on the arrangement of fetal membranes: a single amnion and single chorion, a single chorion, or separate amnion and chorion; dizygous twins have separate amnion and chorion (Falconer 1972).

Conclusions Drawn From Previous Studies

The brief review of previous work indicates that the relative influences of genotype and environment on body weight and skinfold measurements are uncertain. It appears that the phenotypes of weight and skinfold thickness are the manifestations of interactions among genotypic, environmental, and socioeconomic influences. These traits appear to have continuous variation so it is possible that both genetic and environmental factors influence the expression of phenotype. The discrepancies in published estimations of heritability for body weight in

various populations underscore the fact that any heritability estimate is valid only for a particular population at a particular time.

MATERIALS AND METHODS

Estimation of Heritability

The heritability estimate ($\hat{h}^2$) is a statistic commonly used by quantitative geneticists. Its primary function in a breeding program is to reflect the reliability of predicting the breeding values of potential parents based on their respective phenotypic values. The heritability estimate is also used by theoreticians in order to ascertain the possibility of natural selection operating on the character in question. Heritability (h^2) is the population parameter that $\hat{h}^2$ estimates and it can be defined in two manners (Figure 1).

$$h^2_{broad} = V_g/V_p \qquad h^2_{narrow} = V_a/V_p$$
$$V_g = V_a + V_d + V_i$$
$$V_E = V_{Ew} + V_{Ec}$$
$$V_p = V_g + V_E$$

V_g=genotypic variance,V_a=additive variance,V_d=variance due to dominance deviations, V_i=variance due to epistatic interactions,V_E=environmental variance, V_{Ew}=variance within families, V_{Ec}=environmental covariance,V_p=phenotypic variance

Figure 1. Heritability Formulas

Heritability in the broad sense is the ratio of total genotypic variance to total phenotypic variance. Measurement of variance is the preferred method of analyzing dispersion because the genotypic and phenotypic variance can be further subdivided into discrete components. The phenotypic variance can be decomposed into two major components, the genotypic variance and the environmental variance. The genotypic variance can be subdivided further into three parts: variance due to additive effects of genes (breeding values, in the terminology of agricultural genetics), variance due to interaction between alleles at a single locus (dominance deviations), and variance resulting from the interactions among alleles of many loci (epistatic interaction). The environmental variance includes two components, the

environmental covariance (between families), and the environmental variance within families.

Heritability in the broad sense is a purely descriptive parameter that is of little use in a breeding program. Heritability in the narrow sense, the ratio of additive genetic variance to total phenotypic variance, is of far greater utility in a breeding program because the proportion of additive genetic variance reflects the influence of genes that are transmitted from parents to offspring. Heritability in the narrow sense is analyzed rather than heritability in the broad sense because it is genes, not genotypes, that are transmitted from parents to offspring in the form of haploid gametes. The variance components due to dominance deviations and epistatic interactions are not inherited as such.

It should be noted that the heritability of a character is specific for a given population in a given generation. All the components of genotypic variance are influenced by the underlying gene frequencies, which can change from one generation to the next. The environmental variance depends upon the living conditions of the populations. Substantial environmental variance will produce a low heritability value for the trait in question. It is important, therefore, to stress that a given heritability estimate is valid only for a particular population at a specific time.

The heritability estimate is based on the degree of resemblance between different categories of relatives (Table 1). Intra-class correlations determined by an analysis of variance both within and between families are calculated in both sib and half-sib analyses. Regression coefficients are calculated when resemblances between parents and offspring are analyzed.

Each method has certain advantages and disadvantages, and the method of estimation chosen is frequently dictated by the available data set. Half-siblings are relatively uncommon in human populations so that method of analysis is frequently impractical. The full sib correlation is usually the least reliable method because the estimate contains the component of variance due to dominance deviations. The environmental covariance term (Ec) is highest in full sib analysis. These problems may limit the use of full sib estimates to that of setting an upper bound on the heritability of the trait in question. Since the environmental covariance is less in father-offspring pairs than in mother-offspring pairs it is often the desired method of analysis. However, in human populations there is a real possibility of illegitimacy attributable to incorrect assignment of biological paternity. This problem may result in the father-offspring estimate setting a lower bound to the heritability estimate.

Table 1. Methods of Estimating Heritability

Relationship	Proportion of the Variances that the Covariance Measures						Regression b; Intraclass Correlation t
	$\overline{V_i}$						
	V_a	V_d	V_{aa}	V_{ad}	V_{dd}	V_{Ec}	$\hat{h}^2$
Single Parent-Offspring	1/2	—	1/4	—	—	—	2b
Midparent-Offspring	1/2	—	1/4	—	—	—	b*
Sib Analysis	1/2	1/4	1/4	1/8	1/16	1	2t
Half-Sib Analysis	1/4	—	1/16	—	—	—	4t

*since V_p is also halved

When assortative mating is present, the regression of offspring on midparent value is recommended (Falconer 1972). This is because assortative mating causes an increase in the variance of midparent values, resulting in a lower standard error and thus a more precise estimation of heritability. It appears that either the father-offspring or midparent-offspring regression will be the more useful method depending on the human population under examination.

Accurate heritability estimation depends on the ability of the investigator to minimize both the environmental covariance and the standard error of the intraclass correlation or regression coefficient. By definition, the heritability should be within the range of zero to one, although the estimate of this parameter ($\hat{h}^2$) can fall outside this theoretical range due to sampling error. In order for $\hat{h}^2$ to give a close approximation to h^2, the standard error of the heritability estimate should not exceed 0.15. This is because the magnitude of the standard error in part determines the validity of the heritability estimate. To obtain a standard error of 0.15, 150 midparent-offspring pairs or 200 parent-offspring pairs are necessary (Falconer 1963). This level of precision should be considered the lowest allowable level for any experimental design.

With these considerations in mind to obtain the most accurate heritability estimates, part of a continuing study was conducted to estimate heritabilities for various skinfold and body composition parameters in a high-altitude Peruvian population. The population and

measurements will be discussed in the following section. The section after that will explain the statistics and computer methods involved in arriving at the heritability estimates.

Procedures of the Experiment

Camacani is a village in the Department of Puno, Peru. It has approximately 2100 inhabitants and is located at an altitude of 3900 meters above sea level. In 1978, Robert Eckhardt began a study which was to investigate the relative contributions of environmental variation and genotypic variation to the thoracic morphology and nutritional status of this native high-altitude population. The inhabitants are of Aymara ancestry. They are predominantly employed in agriculture and are of Catholic faith; most adults have little formal education.

Children were administered a questionnaire which documented sex, age, place of residence, place of birth, and numbers of brothers and sisters. Adults completed a more extensive questionnaire which also included a list of offspring and other relatives. In addition, adults were administered a general health survey in order to assess cardiovascular performance. A set of 20 anthropometric measurements was taken on both children and adults in order to describe thoracic morphology and nutritional status.

The study was conducted with the goal of measuring at least 200 parent-offspring pairs in order to obtain a standard error of the heritability estimate of 0.15 or less. After low-altitude migrants were removed from the study the sample consisted of 811 individuals, of which 442 were children (from several months to less than 20 years) and 369 adults. These data produced 264 midparent-offspring pairs, 324 father-offspring pairs, and 369 mother-offspring pairs.

Heritability estimates were previously calculated for measurements which defined thoracic morphology (Kramer 1980, also this volume). This study will focus on the heritability estimates of weight, upper arm circumference, subscapular skinfold, suprailiac skinfold, midaxillary skinfold, and triceps skinfold. Subjects were weighed with minimal clothing. The approximate weight of the clothes was then subtracted from the balance value to arrive at the subject's true weight. All skinfold measurements were recorded two seconds after the full pressure of the caliper jaws was applied to the skinfold.

Statistics Analyzed

Heritability estimates were made on body weight and five International Biological Programme (IBP) body composition measurements: upper arm circumference, subscapular

skinfold, suprailiac skinfold, midaxillary skinfold, and triceps skinfold. Midparent-offspring regression was the primary method of analysis utilized in this study. This was to avoid the possibility of underestimating h^2 from father-offspring regression due to whatever illegitimacy might be present in the population. The estimate arrived at by mother-offspring regression may be inflated by maternal effects. The use of midparent-offspring regression may balance the biases inherent in the two other regression methods. This will result in the most reliable estimate of heritability for the available data set.

Heritability estimates were also calculated using full sib correlations even though these estimates contain components of environmental covariance and dominance deviations. The extent of non-additive genetic variance can be estimated by comparing the midparent-offspring heritability estimates with those arrived at by full sib correlations.

Father-offspring and mother-offspring heritability estimates were calculated. The extent to which illegitimacy or maternal effects are present in the population can be revealed by comparing these two estimates.

A problem in the computation of the regression coefficient arises when there are unequal numbers of offspring among parents. Taking each offspring separately and counting the parental value as many times as that parent has offspring gives too much weight to large families. If the unweighted offspring mean is regressed on the parental values the larger families will not be emphasized enough. The method that best utilizes all the data requires the combination of sums of squares and products from families of various sizes. Each family receives a weighting factor determined by the number of offspring in the family. The derivation of this weighting factor can be found in Falconer (1963). The first step is to compute the phenotypic correlation t through an analysis of variance both within and between families. Then an estimate of the regression coefficient b must be calculated. This is done by regressing the unweighted offspring means on the parental values. After estimates of the phenotypic correlation t and regression coefficient b have been obtained it is possible to calculate the weighting factor in two operations. First the variable T must be computed as follows. When the regression is on the mean of both parents

$$T = (t - \frac{1}{2}b^2)/(1 - t),$$

but when regression is made on a single parent

$$T = (t - b^2)/(1 - t).$$

Secondly, the weighting factor, Wn, corresponding to families of n offspring is

$$Wn = (n + nT)/(1 + nT).$$

Another problem involved in the data analysis is that individuals measured were of different sexes and ages. One method of overcoming this problem would have been to make age and sex independent variables along with the offspring value. Multiple regression equations would then be calculated with the three variables. This approach is limited because both age and sex have their own beta coefficient distribution and this introduces two additional error terms into the model. Another method would have been to separate the sexes for both adults and offspring and then to have used growth curves for adjusting all offspring measurements to a single age. One problem of this method is that it results in a loss of data. This loss of data is manifested in the standard error of the heritability estimate. Another difficulty of this approach is that growth curves are uneven because periods of growth spurts do not coincide for all populations. The most efficient method of overcoming differences between ages and sexes is by age-sex standardization of all measurements. Each individual's raw score for a particular parameter was converted into a z-score deviation from the mean of that parameter for a particular age and sex group. This manipulation was performed using a program written in SAS (Appendix A). This standardization introduces only one additional error term into the model and confers several advantages on the analysis. Standardization will correct the problem of unequal variance between sexes. It also removes differences between cohorts with regard to parity. This allows the comparison of siblings of various ages.

Finally, the standard error of the heritability estimate was calculated. It is the magnitude of the standard error that determines how closely $\hat{h}^2$ approximates h^2. It should be noted that the method of analysis utilized influences the magnitude of the standard error. In a midparent-offspring regression the standard error of the regression coefficient equals the standard error of the heritability estimate but if a regression on one parent is employed the standard error of the regression coefficient must be multiplied by two in order to obtain the standard error of the heritability estimate (Falconer 1960). In a full sib analysis the standard error of the heritability estimate is twice the standard error of the intraclass correlation. In a half-sib analysis the standard error must be multiplied by four to obtain the standard error of the heritability estimate (Falconer 1960). The methods used to calculate the standard errors of the intra-class correlations and regression coefficients are described in Falconer (1963).

Once the physical measurements had been converted into z-scores it was possible to calculate heritability estimates. No statistical software packages available to the author perform weighted linear regression, so it was necessary to develop a program to perform the task (Vandemark et al. 1985).

RESULTS

Midparent Heritability Estimates

Regressions of offspring values on midparent values were calculated using the weighted method described in Falconer (1963). Heritability estimates were derived from the calculated regression coefficients. These are listed in Table 2 according to the type of measurement: weight, upper arm circumference, and skinfolds. The standard errors of the heritability estimates are also given.

Table 2. Heritability Estimates Based on Midparent-Offspring Regressions

Trait	$\hat{h}^2$	Standard Error
Body Weight	0.4003	0.0656
Upper Arm Circumference	0.4134	0.0674
Subscapular Skinfold	0.3373	0.0705
Suprailiac Skinfold	0.3208	0.0792
Midaxillary Skinfold	0.2990	0.0636
Triceps Skinfold	0.3249	0.0722

Body weight has a moderate heritability estimate of 0.4003 $\pm$ 0.0656. Upper arm circumference has a slightly higher estimate of 0.4134 $\pm$ 0.0674. The heritability estimates of the skinfold measures are all low to moderate, falling within the range of 0.2990 $\pm$ 0.0636 to 0.3380 $\pm$ 0.0705. Heritabilities of skinfold measurements cluster quite tightly, as they are all within one standard error of each other. Table 3 gives the rank order of heritability estimates for the six parameters under analysis.

It was noted earlier that one objective of the study was to attain heritability estimates with a level of precision such that they would have standard errors of 0.15 or less. The range of standard errors for the six traits is actually considerably lower, ranging from 0.06 to 0.08. As a result, it appears that the available sample made it possible to attain midparent-offspring regressions that were reasonably precise.

Table 3. Rank Order of Heritability Estimates

Trait	$\hat{h}^2$	Trait	$\hat{h}^2$
Upper Arm Circumference	0.4134	Triceps Skinfold	0.3249
Body Weight	0.4003	Suprailiac Skinfold	0.3208
Subscapular Skinfold	0.3373	Midaxillary Skinfold	0.2990

Mother-Offspring and Father-Offspring Heritabilities

Table 4 lists the heritability estimates along with the corresponding standard errors obtained by father-offspring and mother-offspring regressions. Midparent-offspring heritability estimates are given for comparative purposes. The estimates are listed according to the type of measurement: body weight, upper arm circumference, and skinfolds.

Table 4. Mother-Offspring and Father-Offspring Heritability Estimates

Trait	Mother-Offspring $\hat{h}^2 \pm$ S.E.	Father-Offspring $\hat{h}^2 \pm$ S.E.	Midparent-Offspring $\hat{h}^2$
Body Weight	0.5573 ± 0.0973	0.3832 ± 0.1077	0.4003
Upper Arm Circumference	0.5498 ± 0.1002	0.4460 ± 0.1128	0.4134
Subscapular Skinfold	0.3613 ± 0.1021	0.5442 ± 0.1217	0.3373
Triceps Skinfold	0.4457 ± 0.0921	0.2591 ± 0.1071	0.3249
Suprailiac Skinfold	0.4404 ± 0.1073	0.3177 ± 0.1225	0.3208
Midaxillary Skinfold	0.5252 ± 0.0800	0.1370 ± 0.1084	0.2990

In four out of six traits, the midparent estimate is between the maternal and paternal estimates, and the maternal estimate is larger than the paternal estimate. This pattern of results is not surprising; as previously mentioned, the paternal estimates may be reduced due to any existing (even though unknown) illegitimacy in the population. In contrast, mother-offspring regressions may be inflated due to such maternal effects as mothering ability, nutritional status of the mother, and even, in theory, cytoplasmic inheritance (Falconer 1960). The father-offspring heritability estimate for upper arm circumference is lower than the mother-offspring estimate, but slightly higher than the midparent-offspring estimate. The paternal and midparent estimates overlap when the standard errors are considered, so statistical deviations may explain this observation.

The fact that the paternal estimate is much higher than either the maternal or midparent estimates for subscapular skinfold presents a more complex problem in interpretation than the other traits examined in this study. The complication may arise from the nature of the measurement itself, leading to differences between the sexes in measurement deviations. In this high-altitude population, adult females often develop such a large subscapular mass of adipose tissue that it is difficult to get a fold of skin in the caliper. Adult males, on the other hand, do not develop this mass of subscapular adipose tissue and can be easily measured. A more complex causation of the observed results cannot be ruled out until further studies are conducted.

Out of the six traits examined, five have substantially higher maternal estimates than either paternal or midparent estimates; these are body weight, upper arm circumference, suprailiac skinfold, triceps skinfold, and midaxillary skinfold. The mother- offspring estimate is slightly higher than the midparent estimate for subscapular skinfold but the causes of different degrees of maternal effects present remain uncertain.

The standard errors of the father-offspring heritability estimates are in the range of 0.1071 to 0.1225, whereas the standard errors for the mother-offspring heritability estimates range from 0.0800 to 0.1021. The differences between maternal and paternal standard errors are substantially due to a larger sample of mother-offspring groups than father-offspring groups, since the magnitude of the standard error is inversely related to the sample size (Falconer 1960).

<u>Comparison of Sib Analysis Heritabilities with Those Derived from Other Relationships</u>

Although a heritability estimate derived from a sib analysis will contain components of common environmental variance and nonadditive genetic variance, it is still a useful statistic. Comparison of heritability estimates derived from sib analyses with those derived from alternative methods gives an indication of the effects of common environment and nonadditive genetic variance on the traits in question. Table 5 lists the heritability estimates derived from sib analyses for the six parameters included in this study, along with maternal and midparent estimates for comparative purposes.

Table 5. Heritability Estimates Derived From Sib Analysis With Comparative Estimates

Trait	Sib Analysis $\hat{h}^2 \pm$ S.E.	Maternal $\hat{h}^2$	Midparent $\hat{h}^2$
Body Weight	0.4418 ± 0.1080	0.5573	0.4003
Upper Arm Circumference	0.5985 ± 0.1105	0.5498	0.4134
Subscapular Skinfold	0.4721 ± 0.1804	0.3613	0.3373
Triceps Skinfold	0.3577 ± 0.1084	0.4457	0.3249
Suprailiac Skinfold	0.3892 ± 0.1095	0.4404	0.3208
Midaxillary Skinfold	0.3354 ± 0.1106	0.5252	0.2990

Weight has a maternal estimate which is greater than the sib estimate, which in turn is larger than the midparent estimate. This indicates that little or no nonadditive genetic variance is present, but that maternal effects may influence the body weight of offspring. The sib estimate is within one standard error of the midparent estimate. Very similar results were found by comparison of sib estimates with maternal and midparent estimates for midaxillary skinfold, triceps skinfold, and suprailiac skinfolds. This indicates that maternal effects may influence the expression of these three traits, and that little nonadditive genetic variance is present.

For upper arm circumference, the sib estimate is the largest, followed by the maternal estimate, with the midparent estimate being the smallest in magnitude. The maternal estimate is within one standard error of the sib estimate, so maternal effects may explain the majority of nonadditive similarities. Upper arm circumference is the parameter most widely

used in hospitals to assess the nutritional status of patients (Burgert and Anderson 1979). This single measurement includes a cross-section of different tissues: bone, muscle, fat, and skin. Nonadditive genetic variation could contribute to the development of any or all of these tissues which comprise the upper arm circumference measurement.

The sib estimate for subscapular skinfold may help to solve the problems resulting from the estimates arrived at by regression techniques. The series of heritability estimates for subscapular skinfold, in descending order, is as follows. The paternal estimate is greater than the sib estimate which is greater than the maternal estimate; the midparent estimate is the smallest. The sib estimate is within one standard error of the paternal estimate, so it is possible that the high paternal estimate is not an artifact. The most reliable estimate of the subscapular skinfold heritability may be the average of estimates derived from repeated measurements on each subject. From the available results it appears that a conservative estimation of heritability for subscapular skinfold would be 0.40 ± 0.15. This should be considered as only a tentative estimate until the questions involving subscapular skinfold measurements are resolved by further studies.

The standard errors of the heritability estimates derived from sib analyses were all within the range of 0.1080 to 0.1106. The close range of standard error may partially be due to nearly equal sample sizes for all the sib analyses.

Summary of Results

Table 6 summarizes the results discussed in this section. As stated previously, the midparent-offspring regression coefficient is the statistic employed in estimating heritability. This is because the mother-offspring estimate may be inflated due to maternal effects and the father-offspring estimate may be reduced due to the presence of illegitimacy within the population. The next section will discuss the implications of these results.

DISCUSSION

The credibility of results arising from a human quantitative genetic study must be carefully scrutinized. This is because human studies cannot accept certain conditions that are taken for granted in plant or animal experimental designs. For example, the animal breeder can be virtually certain that his records do not contain incorrect pedigree information because of illegitimacy within the population. The occurrence of an illegitimate birth in a human

Table 6. Summary of Results for the Heritability Estimates

Trait	$\hat{h}^{2*}$	Magnitude	Nonadditive Effect Present
Body Weight	0.4003	Moderate	Maternal effects
Upper Arm Circumference	0.4134	Moderate	Maternal effects, possibly some non-additive genetic variance
Subscapular Skinfold	0.3373	Low to Moderate	Unclear
Triceps Skinfold	0.3249	Low to Moderate	Slight maternal effects
Suprailiac Skinfold	0.3208	Low to Moderate	Slight maternal effects
Midaxillary Skinfold	0.2990	Low to Moderate	Maternal effects

*Midparent estimate

population, not at all an uncommon event, may not be acknowledged by the mother for reasons of social acceptance, and may not be recognized by the socially-designated father.

A heritability estimate is both population and temporally specific. Changes in way of life, due to factors in the natural or cultural setting, can accordingly change the environmental variance. This can theoretically result in differing heritability estimates for a particular population at two different times.

A problem inherent in skinfold measurements, in particular, is variation within and between technicians. Coefficients of variation for five skinfold measurements within technicians of the U.S. Health Examination Survey varied from 15.4% (triceps) to 17.7% (suprailiac), while those between technicians varied from 6.5% (triceps) to 24.5% (midaxillary) according to the work of Malina (1980).

It was stated previously that the original expectation was for the maternal estimate to be larger than the midparent estimate, which would in turn exceed the paternal estimate. This expectation was borne out in four out of six traits, and upper arm circumference deviated only slightly from this anticipated pattern. The slightly higher value of the upper arm circumference based on the paternal estimate, which exceeds the midparent estimate, may

reflect sampling deviations. In any case, the upper arm circumference maternal estimate is substantially larger than both the paternal and midparent estimates.

The results derived for subscapular skinfold had adequately small standard errors but are not easily interpreted. Further studies will have to be performed in order to determine whether the inflated paternal estimate is the result of sampling deviations or a more complex, as of yet undiscovered, mechanism.

The sib correlation should have been the highest estimate for a particular trait because the heritability estimate derived from a sib analysis contains components of common environment and dominance deviations (Falconer 1960). This was the case for only one out of the six traits (upper arm circumference), but all six traits had higher heritability estimates from sib correlations than from midparent-offspring regressions. Therefore, inferences from these results must be drawn cautiously. All the sib estimates had standard errors that are low by general standards.

Considering the limitations inherent in a human quantitative genetics study, the resulting heritability estimates appear plausible and have acceptable standard errors.

Interpretations Arising from the Heritability Estimates

Of the six traits analyzed, four showed a common pattern, in which the heritability estimate based on the mother-offspring regression exceeded the estimate based on the midparent-offspring regression (body weight, midaxillary skinfold, triceps skinfold, and suprailiac skinfold). The maternal and midparent estimates are not significantly different when the standard errors are considered, so sampling deviations cannot be ruled out as the cause of these inflated maternal estimates. However, the observed patterns are consistent with suggestions of the presence of a modest maternal effect operating on these traits.

The only trait where an appreciable amount of nonadditive genetic variance may be present is upper arm circumference. For this trait, the sib estimate is greater than the maternal estimate, and both exceed the midparent estimate. The sib estimate and maternal estimate are not significantly different when the standard errors are considered, suggesting that maternal effects may explain most of the nonadditive similarities. Upper arm circumference includes a cross-section of different tissues: bone, muscle, fat, and skin. Nonadditive genetic variation could contribute to the development of any or all of these tissues which comprise the upper arm circumference measurement.

The results derived from subscapular skinfold measurements are not easily interpretable. The inflated paternal estimate may be the result of sampling deviations or due

to a more complex mechanism which results in an increased resemblance between father and offspring. Consequently, the most reliable estimate of the subscapular skinfold heritability may be the average of estimates derived from repeated determinations.

Extension of Results

The purpose of this study was to calculate heritability estimates in order to assess the amount of additive genetic variation in the traits which reflect the nutritional status of native high-altitude Peruvians. As noted earlier, the conclusions drawn from previous studies have left unresolved the relative influences of environment and genotype on growth and development in Andean populations. This is not surprising considering the difficulties involved in quantitative genetic analyses of human populations, as well as the many factors responsible for variation in human nutritional conditions.

The midparent heritability estimates for all six of the traits analyzed were within the range of 0.2990 to 0.4134, and had relatively low standard errors. This indicates that a moderately heritable component may be present in these traits which define nutritional status. There are several possible reasons for this moderate heritability estimate. The first is that in the past, natural selection operated on the trait in question to reduce the amount of additive genetic variance. This reason may plausibly explain the observed results. For instance, it has been noticed that a female's nutritional status and amount of adipose tissue is directly related to age at menarche and probability of a continuous ovulation (Hussein et al. 1984, Prader 1984). These two factors indirectly affect fertility rates in women.

Other available heritability estimates for weight are all from sea level populations and are all higher than the observed estimate of 0.4003 $\pm$ 0.0656 for this Andean population. The Greek population studied by Klissouras (1984) had a heritability estimate of 0.80 for body weight; an Indian population analyzed by Devi and Reddi (1983) yielded an estimate of 0.541. The estimate of Susanne (1977) for a Belgian population was 0.625, and that of Clark (1955) for a Michigan population was 0.69. Roberts (1953) demonstrated that increasing cold is accompanied by an increase in weight. The significantly lower heritability estimate of the high-altitude population relative to previous sea level estimates, coupled with the reduced weight of high-altitude Peruvians despite the cold environment, suggests that natural selection could be operating on the population. A smaller body weight could be of significant advantage in the hypoxic Andean environment. However, it is possible that the reduced weight in the population is the result of limited food supply in the village. It was noted earlier that the average male inhabitant of Nuñoa weighed approximately five kg less than his

counterpart in Camacani (Eckhardt and Dutt 1979). This difference cannot be attributed to altitude since both villages lie at approximately 3900 meters. Preliminary nutritional studies indicate that the inhabitants of Nuñoa may have an inadequate diet as compared to the diet of residents of Camacani (Mazess and Baker 1964, Gursky 1969, Eckhardt and Dutt 1979).

It should be noted that other evidence exists for natural selection operating on this population. Kramer (1980 and this volume) calculated heritability estimates of traits which defined the Andean thorax for the same population under investigation here. The three chest traits which contribute most directly to the observed difference between highland and lowland natives had moderate heritability estimates: sternal length, anterior-posterior diameter thorax, and anterior-posterior diameter substernal. Response to selection may have contributed to the differences in chest size between lowland and highland natives.

Another possible reason for the moderate heritability estimates observed in this population is that a high amount of environmental variation may be present in the traits analyzed. It has clearly been demonstrated that an increase in physical exercise levels results in a decrease in the amount of body fat (Oscai et al. 1974, Parizkova 1973). An examination of the rank order of heritability estimates for this population indicates that the traits associated with adipose tissue seem to be affected more by environmental influences than traits associated with bone and muscle. For example, in this population, the trait with the highest heritability estimate, $\hat{h}^2 = 0.509 \pm 0.135$, is stature (Kramer 1980 and this volume). This is followed by upper arm circumference (0.4134), body weight (0.4003), subscapular skinfold (0.3373), triceps skinfold (0.3249), suprailiac skinfold (0.3208), and midaxillary skinfold (0.2990). Stature is most directly dependent on skeletal structure. Short term changes in caloric intake or proportions of fat, protein, and carbohydrate in the diet may have more effect on tissues such as fat and muscle than on skeletal components. Upper arm circumference and body weight both consist of bone, muscle, and skin. The two heritability estimates are very close and may reflect similarities in the effects of nutritional changes on the values of these measurements. The four skinfold estimates are all very similar to one another, yet are quite a bit smaller than the estimates for upper arm circumference and body weight. These measurements reflect elements of skin and fat. The low heritability estimates obtained here appear to indicate that the skinfold measures are the most susceptible to changes in dietary patterns or levels of physical activity.

The relative amounts of genetic and environmental variance present in these traits will remain uncertain until further studies are completed. One future avenue for further research would derive heritability estimates from families in which one parent is native to high

altitude and the other parent is native to low altitude. Reciprocal studies of this type may help to determine the relative effects of environment and genotype on these traits. The use of repeated measurements may reduce errors and yield more valid heritability estimates.

CONCLUSIONS

Heritability estimates were calculated for six anthropometric traits in a high-altitude Peruvian population. From these estimates it is possible to assess the amount of heritable variation present in these traits. The imposed limit of accuracy of a standard error less than 0.15 was achieved for all 24 estimates, thus indicating a sufficient sample size was analyzed. Previous studies have suggested the presence of significant environmental influences on these traits. The low heritability estimates derived for the four skinfold measures indicate that a substantial component of environmental variance may be involved in adaptation to a high-altitude environment.

Other studies suggested the presence of a heritable component in the traits which define the Andean nutritional status. The results of this study indicate that the highest observed heritability estimates were for the traits that best defined nutritional status: body weight and upper arm circumference. These values, however, could be the result of environmental changes having less influence on these traits than on skinfold measurements.

From the results reported here, it can be concluded that there is sufficient additive genetic variation on which natural selection could act to influence the body weight and nutritional status of this high-altitude population. If the hypoxic stress were present in the past, then it is possible to understand how natural selection might have acted on the population to reduce body weight in response to the stress of a hypoxic environment.

Appendix A

SAS PROGRAM TO CONVERT VALUES TO AGE AND SEX SPECIFIC Z-SCORES

```
CMS FILEDEF TEMP  DISK AYMARA INPUT A;
DATA HALT;

                    note:this reads data from an input
                         file called 'aymara input a'.
INFILE TEMP;
   INPUT SN 1-4 WT 7-11 2 UAC 12-14 1 SS 15-17 1 SIS 18-20
         1 MAS 21-23 1 TS 24-26 1 AGE 27-30 1 SEX 31 ;

   note: sn = subject number.
         wt = body weight.
         uac = upper arm circumference.
         ss = subscapular skinfold.
         sis = suprailiac skinfold.
         mas = midaxillary skinfold.
         ts = triceps skinfold.



   note: the following section of this program
         orders the subjects into age groups.

IF AGE > 0 AND AGE <1.4 THEN AG=1;
IF AGE >=1.4 AND AGE<2.7 THEN AG=2;
IF AGE >=2.7 AND AGE<4 THEN AG=3;
IF AGE >=4 AND AGE<5 THEN AG=4;
IF AGE >=5 AND AGE<6 THEN AG=5;
IF AGE >=6 AND AGE<7 THEN AG=6;
IF AGE >=7 AND AGE<8 THEN AG=7;
IF AGE >=8 AND AGE<9 THEN AG=8;
IF AGE >=9 AND AGE<10 THEN AG=9;
IF AGE >=10 AND AGE<11 THEN AG=10;
IF AGE >=11 AND AGE<12 THEN AG=11;
IF AGE >=12 AND AGE<13 THEN AG=12;
IF AGE >=13 AND AGE<14 THEN AG=13;
IF AGE >=14 AND AGE<15 THEN AG=14;
IF AGE >=15 AND AGE<16 THEN AG=15;
IF AGE >=16 AND AGE<17 THEN AG=16;
IF AGE >=17 AND AGE<18 THEN AG=17;
IF AGE >=18 AND AGE<19 THEN AG=18;
IF AGE >=19 AND AGE<20 THEN AG=19;
IF AGE >=20 AND AGE<25 THEN AG=20;
IF AGE >=25 AND AGE<30 THEN AG=21;
IF AGE >=30 AND AGE<35 THEN AG=22;
IF AGE >=35 AND AGE<40 THEN AG=23;
IF AGE >=40 AND AGE<45 THEN AG=24;
IF AGE >=45 AND AGE<50 THEN AG=25;
IF AGE >=50 AND AGE<55 THEN AG=26;
IF AGE >=55 AND AGE<60 THEN AG=27;
IF AGE >=60 AND AGE<65 THEN AG=28;
```

```
IF AGE >=65 AND AGE<70 THEN AG=29;
IF AGE >=70 AND AGE<75 THEN AG=30;
IF AGE >=75 AND AGE<85 THEN AG=31;
IF AGE >=85 AND AGE<100 THEN AG=32;

PROC SORT;   note:this sorts values into age and sex groups.
BY SEX AG;

PROC PRINT;  note:this prints values into age and sex groups.
BY SEX AG;
VAR SN AGE WT uac ss sis mas ts ;

note:the following proceedure converts the observations in each
      age and sex specific group to z-scores.

PROC STANDARD MEAN=0 STD=1 OUT=NEW;
BY SEX AG;
VAR    AGE WT UAC SS SIS MAS TS ;

PROC SORT DATA=NEW;   note:this sorts subjects by i.d. numbers.
BY SN;

PROC PRINT DATA=NEW;  note:this prints z-scores for each subject.
BY SN;
VAR SN WT UAC SS SIS MAS TS;
```

Appendix B

REGRESSION ANALYSIS WITH WEIGHTED COFACTORS

```
{ This program will be used in order to calculate heritability }
{ estimates by the technique of weighted regression analysis.  }
{ The use of a weighted factor allows different size families  }
{ to be included in the sample used for heritability analysis. }
{ the experimentor must change the constant 'maxfam' to the    }
{ amount of families to be analyzed and after the final child's}
{ value for each family has been inputted the dummmy variable   }
{ -9.0 must be inputted so that the number of offspring per     }
{ family can be assertained. This method can be utilized for    }
{ either sire-offspring,dam-offspring or midparent-offspring    }
{ regression analysis by inputting a '1' for sire or dam        }
{ regression or by inputting a '2' for midparent regression     }
{ in the first space of the input file. This method can be      }
{ reviewed in 'Manual of Quantitative Genetics'.1975. Walter    }
{ A. Becker, Washington State University Press.                 }
```

```
program regway (input, output);
const maxfam = 200;
type parent=(onepar,midpar);
var family : array (.1..maxfam,1..8.) of real;
    children : array (.1..maxfam,1..15.) of real;
    i,j : integer;
    sumksum,sumkssq,betsire,maxkids,skfamsq,psum,psumsq,psumksum,
    ksumsq,fksumsq,temp,ksum,tempsq,mean,meansq,pksq,meankids,
    kmeansq,kidfam,kidfsq,fambs,corrterm,sumsqbt,sumsqwth,meansqbt,
    meansqw,k,sigsqbt,tofher,spsumsq,xzpern,sumsubxz,herit,capt,
    weight,wxy,wx,wy,wxsq,wysq,capwxy,capwxsq,trueher,capwysq,
    variance,sumwxy,sumwx,sumwy,sumw,sumwxsq,sumwysq : real;
    thispar :parent;
    index : integer;
    sterror, beta : real;

begin
    sumksum:=0.0;   { sum of offspring values for all families. }
    sumkssq:=0.0;   { sum of offspring values squared, all families.}
    betsire:=0.0;   { between mid parent uncorrected sum of squares.}
    maxkids:=0.0;   { number of offspring totaled for all families. }
    skfamsq:=0.0;   { sum of offspring number squared for all families.}
    psum:=0.0;      { sum of mid parent values for all families.}
    psumsq:=0.0;    { sum of mid parent values squared for all families.}

    psumksum:=0.0;  { sum of midparent * mean of offspring for all fams}
    sumksum:=0.0;
    ksumsq:=0.0;    { sum of offspring means squared for all families.}
    sumwxy:=0.0;    { sum of weighting factor*midparent*offspring mean.}
    sumwx:=0.0;     { sum of weighting factor * midparent, all families.}
    sumwy:=0.0;     { sum of weighting factor * offspring mean. }
```

```
sumw:=0.0;        { sum of weighting factors for all families.}
sumwxsq:=0.0;     { sum of weighting factor*midparent squared. }
sumwysq:=0.0;     { sum of weighting factor*offspring mean squared.}
read (index);
if index = 1
  then thispar:= onepar
        else if index = 2
            then thispar:= midpar;

for i:=1to maxfam do
     begin
         if thispar = onepar then read (family(.i,1.))
         else if thispar = midpar
         then read (family(.i,1.),family(.i,2.));
         ksum:=0.0;
         fksumsq:=0.0;
         j:=1;
         read (temp);
          while temp <>-9.0 do                  { This loop evaluates the }
                begin                            { number off offspring per}
                   children(.i,j.):=temp;        { family.}
                   ksum:=ksum+temp;
                   tempsq:=temp*temp;
                   fksumsq:=fksumsq+tempsq;
                   j:=j+1;
                   read (temp)
                end;

         family(.i,3.):=ksum;
         sumksum:=sumksum+ksum;
         family(.i,4.):=j-1;
         if thispar = onepar
         then family(.i,6.):= family(.i,1.)
         else if thispar= midpar
               then family(.i,6.):= (family(.i,1.)+family(.i,2.))/2.0;

         family(.i,7.):=ksum/family(.i,4.);
         mean:=family(.i,6.);
         psum:=psum+mean;
         meansq:=family(.i,6.)*family(.i,6.);
         psumsq:=psumsq+meansq;
         pksq:=family(.i,6.)*family(.i,7.);
         psumksum:=psumksum+pksq;
         meankids:=family(.i,7.);

         kmeansq:=family(.i,7.)*family(.i,7.);
         ksumsq:=ksumsq+kmeansq;
         family(.i,5.):=fksumsq;
         sumkssq:=sumkssq+fksumsq;
         kidfam:=family(.i,4.);
         maxkids:=maxkids+kidfam;
         kidfsq:=family(.i,4.)*family(.i,4.);
         skfamsq:=skfamsq+kidfsq;
         fambs:=(family(.i,3.)*family(.i,3.))/family(.i,4.);
```

```
            betsire:=betsire+fambs
            end;


corrterm:=(sumksum*sumksum)/maxkids;
sumsqbt:=betsire-corrterm;          {corrected sum of squares between}
sumsqwth:=sumkssq-betsire;          {corrected sum of squares within.}
meansqbt:=sumsqbt/(maxfam-1);       {mean square bet offspring groups}
meansqw:=sumsqwth/(maxkids-maxfam); {mean square wthn offspring group}
k:=1/(maxfam-1)*(maxkids-(skfamsq/maxkids));  {coefficient K sub i}
sigsqbt:=(meansqbt-meansqw)/k;      {variance between offspring group}
tofher:=sigsqbt/(sigsqbt+meansqw);  { phenotypic correlation }
spsumsq:=psumsq-(psum*psum)/maxfam; { sum of small case 'x' squared.}
xzpern:=(psum*sumksum)/maxfam;      .{(sum X * sum Y)/number families}
sumsubxz:=psumksum-xzpern;          { sum small 'x'* small 'y' }
if thispar = onepar
then herit := (sumsubxz/spsumsq)*2.0
 else if thispar= midpar
      then herit := sumsubxz/spsumsq;
if thispar = onepar
then capt := (tofher - (herit*herit))/(1-tofher)
   else if thispar = midpar
   then capt := (tofher-(herit*herit)/2.0)/(1-tofher);


{ This loop calculates the weighting factor for each family and }
{ puts this value in the matrix position (.i,8.) so that it can }
{ be accessed in order to compute the true heritability value.  }

for i:=1to maxfam do
    begin
      weight:=(family(.i,4.)+family(.i,4.)*capt)/(1+family(.i,4.)*capt);
       family(.i,8.):=weight;
       wxy:=family(.i,8.)*family(.i,7.)*family(.i,6.);
       sumwxy:=sumwxy+wxy;
           wx:=family(.i,8.)*family(.i,6.);
       sumwx:=sumwx+wx;
       wy:=family(.i,8.)*family(.i,7.);
       sumwy:=sumwy+wy;
       weight:=family(.i,8.);
       sumw:=sumw+weight;
       wxsq:=family(.i,8.)*(family(.i,6.)*family(.i,6.));
       sumwxsq:=sumwxsq+wxsq;
       wysq:=family(.i,8.)*(family(.i,7.)*family(.i,7.));

       sumwysq:=sumwysq+wysq
    end;

capwxy:=sumwxy-((sumwx*sumwy)/sumw);
capwxsq:=sumwxsq-((sumwx*sumwx)/sumw);
beta := capwxy/capwxsq;
if thispar = onepar
  then trueher:= 2.0*(capwxy/capwxsq)
else if thispar = midpar
  then trueher:= capwxy/capwxsq;
```

```
capwysq:=sumwysq-((sumwy*sumwy)/sumw);
variance:=(1/(sumw-2))*((capwysq/capwxsq)-beta * beta);
if thispar = onepar
   then sterror := 2.0*(sqrt(variance))
else if thispar = midpar
  then sterror:= sqrt(variance);
write('The heritability equals ',trueher:6:4,' +- ',sterror:6:4);
writeln;

write('ksum','    number of kids','       meankids','      weight');
writeln;
for i:=1 to maxfam do
     begin
        writeln(family(.i,3.):4:2,'        ',family(.i,4.):4:2,'
            ',family(.i,7.):4:2,'                  ',
                family(.i,8.):10:8)
     end;
end.
```

APPENDIX C

PHENOTYPIC CORRELATIONS (t) AND UNWEIGHTED BETA COEFFICIENTS (b)
COMPUTED WITH VARIOUS REGRESSION METHODS

Trait	Method	t	b
Body Weight	Midparent-Offspring	.2281	.4249
	Mother-Offspring	.2453	.2564
	Father-Offspring	.2495	.2222
Upper Arm Circumference	Midparent-Offspring	.3008	.4543
	Mother-Offspring	.3347	.3022
	Father-Offspring	.3078	.2464
Subscapular Skinfold	Midparent-Offspring	.2155	.3426
	Mother-Offspring	.2463	.1823
	Father-Offspring	.2954	.2973
Suprailliac Skinfold	Midparent-Offspring	.2214	.4062
	Mother-Offspring	.1905	.2527
	Father-Offspring	.2196	.2061
Midaxillary Skinfold	Midparent-Offspring	.2009	.3382
	Mother-Offspring	.1994	.3123
	Father-Offspring	.2097	.0714
Triceps Skinfold	Midparent-Offspring	.2623	.3159
	Mother-Offspring	.2408	.2179
	Father-Offspring	.2390	.1186

CHAPTER 6

HERITABILITY ESTIMATES OF FOUR ANTHROPOMETRIC MEASUREMENTS ON THE THORAX IN A HIGH ALTITUDE PERUVIAN POPULATION

Young Im Ahn

ABSTRACT

Human populations at high altitude in the Andes exhibit distinctive morphological and physiological features which distinguish them from their counterparts at sea level. One of the most striking features is a large chest relative to stature in high-altitude natives. The determinants of this adaptation are uncertain. Some studies suggest that the adaptive complex is the result of developmental acclimatization each generation in response to environmental stresses. Other studies propose that the phenotypic distinctions result from genetic influences shaped by natural selection. Selection cannot cause evolutionary change in a quantitative trait unless additive genetic variation is present. The objective of this paper is to estimate the proportion of additive genetic variance present in the traits which describe body and chest morphology in the Andean population under study.

In this study, anthropometric measurements of body size and chest size were taken on a Peruvian population in Camacani, Peru, at an altitude of 3900 m. The raw measurements were transformed to age- and sex-specific z-scores. Heritability estimates for these measurements were derived from midparent-offspring regression, mother-offspring regression, father-offspring regression, and sib intraclass correlation. For the traits concerned, the heritability estimates are low to moderate. It can be concluded that a substantial amount of environmental variance influences the variation in body size and chest morphology of the Andean population, but that measurable levels of genetic variance are present as well.

INTRODUCTION

Andean Environment and Population

The central Andes mountains rise abruptly between the Pacific ocean and the Amazon basin. The average altitude of the Andes is 4880 m and the highest elevation is 6550 m. The formation of these mountains began approximately 5 million years ago with uplift during the Pliocene and Pleistocene (Jenks 1956). The resulting short geological history has produced a

rugged topography and immature soil. The Andes curve from the northern coast of Venezuela around the western margin of the continent, southwest through Colombia and Ecuador, southeast through Peru, and due south for the full length of Chile (Thomas and Winterhalder 1976). Along the western coast of the mountains is a desert with a sparse loma (fog-moistened hilltop) vegetation. The eastern escarpment, in contrast, with its equatorial warmth and rainfall, produces tropical forests. Between, in the mountains and intermontane valleys, is a patchwork of habitats ranging from desert to rain forest and coastal to alpine. Several chains of Andean mountains separate in central and southern Peru, eastern Bolivia, and northern Chile to accommodate broad high-altitude valleys and plateaus collectively known as the *altiplano*. The altiplano comprises the central Andean high tableland surrounding Lake Titicaca and Lake Poopo, above 3660 m of altitude (Pearson 1951).

The following description of the Andean climate is based on Eidt (1968). Precipitation is seasonal in the altiplano; rainfall begins in September, reaches a peak intensity in January, and ends in April. Moist air from the south Atlantic anticyclone is blown west and releases its moisture on the eastern side of the Andes. The barometric pressure and temperature of this air increase as it moves down the westward slope of the Andes, augmenting its capacity to hold water. This downward flowing air mass desiccates the altiplano by evaporating moisture from vegetation and soil; as a result, droughts up to one year are common in the altiplano. Droughts resulting from irregular monthly precipitation can be equally devastating if they occur during September or October, the beginning of the planting season. The altiplano in general has a constant mean temperature because of its location within the earth's tropical region. During the period from 1931 to 1972 the monthly mean maximum temperature was 17.3° C with a monthly mean minimum of -3.0° C; the range was 20.7° C (Thomas and Winterhalder 1976).

The altiplano exhibits extreme diurnal temperature variation because of the lack of vegetation and thin atmosphere associated with high altitude. The daily high temperature of approximately 17° C occurs in the afternoon, and on clear nights the temperature may fall below freezing. This diurnal variation results in the possibility of frost occurring during any time of the year.

At high altitude unpleasant physiological and psychological reactions are experienced by newcomers or sojourners. These include a shortness of breath with respiratory distress and hyper-ventilation, a rapid pulse rate, interrupted sleep, and headaches intensified by activity, as well as severe physical and mental fatigue (Mongé and Mongé 1966, Frisancho 1975, Heath and Williams 1977). However, the intensity of these symptoms varies among individuals.

The altiplano imposes, in fact, a whole set of environmental stresses. Clegg et al. (1970) and Heath and Williams (1977) have described the reduced air temperature, increased solar base and the reduced partial pressure of oxygen in the ambient air. On the other hand, Thomas (1976) has suggested that there are, as additional potential stresses, rugged topography and poorly developed soil, sharp diurnal temperature variation, intense frosts, and the irregular monthly precipitation distribution. This combined list includes only some of the more evident environmental stresses present at high altitude.

Of all these stresses, hypoxia is the most pervasive in the Andes. Hypoxia can, in fact, be produced by any physiological, pathological or environmental condition that interferes with the oxygen supply to the tissues, as seen in many diseases such as chronic bronchitis and emphysema. Hypoxia can also be produced by normal depletion of oxygen in the atmosphere such as occurs at high altitudes. At sea level, the barometric pressure is 760 mm Hg and the partial pressure of oxygen (pO_2) is 159 mm Hg; at 3500 m the pressure is 493 mm Hg and pO_2 is 103 mm Hg. Thus, at an altitude of 3500 m, the oxygen has about 35% less pressure than at sea level. Because of this reduction of pO_2, the oxygen content of the air reaching the trachea and alveoli is also reduced and this, in turn, reduces the amount of oxygen that is available to the tissues. At high altitude, therefore, hypoxia is an enduring aspect of existence, a condition not caused by pathology and not alleviated to any significant extent by cultural adjustments.

It would seem that the Andean high plateau was peopled at least 10,000 years ago, and perhaps as much as 20,000 years ago (Vellard 1976). Vellard's (1976) classification of human groups now living on the Peruvian-Bolivian altiplano is based on the hypothesis of successive waves of immigrants. A few groups (Urus, Chipayas) are descended from the oldest Andean natives (referred to as the Laguides) that were pushed back to the most inhospitable zones. The Altiplanides or Aymaras, who people the north zone of the inter-Andean corridor and have never wandered far away from it, go back to the hunters who drove back or assimilated the first populations of the high plateau. They have preserved their linguistic, cultural, and social uniqueness in the same ecological milieu. The Andides or Quechuas, heirs to the great Inca culture, predominate numerically, territorially, and socially over the others. Their ecological milieu extends beyond the higher Andean zones to the neighboring valleys. They differ from the preceding two groups in that they appear less well adapted to high altitude and are far less homogeneous (Arnaud et al. 1985).

A brief discussion of the diet of Andean populations is pertinent here since the data treated in this chapter comprise measurements taken on highlanders during various stages of growth. The Peruvian Andes can be divided into two major ecological zones. The sierra consists

of lands from sea level to 3200 m (Picón-Reátegui 1976). The cultivation of cereals, tubers, sugar cane, bananas, and other crops is possible within this range of altitude. The resultant dietary diversity may be a primary cause of the long history of dense habitation of the Peruvian sierra. The second zone, the puna, consists of two subzones, the jalca (found chiefly in the northern Peruvian Andes) which begins at 3200 m, and the true puna (found in the central and southern Peruvian Andes) which begins at approximately 3800 m (Picón-Reátegui 1976). Natural pasture grows in the jalca, but agriculture in the true puna is restricted by poor soil and cold temperatures. Only potatoes and species of the genus *Chenopodium*, such as quinoa, can successfully grow in the true puna (Picón-Reátegui 1976). Generally poor transportation has traditionally restricted dietary diversity; for generations, the populations in this area have been reliant primarily on local food sources.

Gursky (1969) conducted a substantial quantitative analysis of the high-altitude Peruvian diet in the town of Nuñoa, which lies at an altitude of about 4000 m. This data indicated that the typical native diet derived 86% of the total caloric intake from carbohydrates, 8.1% from proteins, and 5.6% from fats. Vegetable products accounted for 93.7% of the total mass of the diet, of which over 80% was either potatoes or quinoa. These values can be taken only as gross estimates because there is some seasonal variation in the diet associated with harvesting cycles.

Compared to European and American populations, the diet of high altitude Andean populations is high in carbohydrates and low in fats (Picón-Reátegui 1978). Caloric and nutrient components of the diet may meet the recommended allowances just after harvesting, but tend to become more and more deficient as the next harvest is approached. The situation has substantial impact on certain segments of the community: children, old people, and pregnant and lactating women.

No quantitative analysis has been conducted on the Camacani community from which the sample population for this study was derived. However, in view of certain environmental factors such as a more temperate lakeshore environment, the average nutritional level in this settlement very probably exceeds that in Nuñoa. Dietary staples in Camacani include potatoes and quinoa as in Nuñoa, but its proximity to Lake Titicaca makes the exploitation of animal protein sources easier than in Nuñoa. Fish are available to Camacani residents, who also use the reeds which border the shore as food for livestock, chiefly dairy cattle. It is probable that the inhabitants of Camacani consume more animal products per capita than those of Nuñoa, including more fat as well as protein. The apparently greater nutritional adequacy of the Camacani diet relative to the Nuñoa diet may be inferred in part from the observation that the

average Camacani male weighs 5 kg more than his Nuñoa counterpart (Eckhardt and Dutt 1979), though divergent ancestry may be a confounding factor. Different levels of physical activity between the two populations probably cannot account for all of the observed differences in body weight because males of both populations spend approximately 12 to 14 hours a day engaged in pastoral or agricultural labor (Picón-Reátegui 1976).

Genetics of Andean Populations

According to population genetic theory, it cannot be presumed *prima facie* that two or more human groups derived from a common ancestral breeding population, speaking the same language, and being similar culturally, must necessarily possess similar gene pools (Garruto et al. 1976). If there has been even partial isolation and the habitats of the populations have been dissimilar, given a sufficient period of time there is the possibility that significant genetic differentiation at some loci may exist due to differential selective pressures, gene flow from other gene pools, migration, and genetic drift in subpopulations (Wright 1931, 1948, 1978).

Garruto and Hoff (1976) have outlined some of the factors governing the genetics of the Quechua population in Nuñoa, Peru, the most extensively described Andean highland group. Quechua speakers are distributed over an area that corresponds roughly to the Andean portions of the ancient Inca Empire at the zenith of its military expansion. It can be assumed that factors such as degree of isolation, breeding patterns, selection pressures, demography, and random events have operated jointly to affect both the genetic structure of the Nuñoa population and its genetic affiliation with other Quechua groups in this area of Peru. Among other factors, the size of the population and especially its effective breeding size are influential in affecting a number of genetic parameters. For example, the smaller the breeding size, the more the population is subject to the decay of genetic variation as a result of a reduction in mate choice leading to inbreeding. This factor may be not significant (at least over the short term) in affecting the genetics of the Nuñoa population, since Dutt (1976) has shown that the amount of gene flow into the population appears to be more than sufficient to counteract genetic drift. The patterns of gene flow are affected by marriage patterns (which influence movement of people within the population) and the fiesta system (which involves movement of people from nearby populations), as well as migration across broader regions.

Another factor that may be important in many altiplano Quechua populations is the moderate to strong selective pressure that could be produced by high mortality rates in the young. The upper limits of postnatal selection intensity can be estimated through the use of Crow's (1958) formula, usually referred to as the Index of Opportunity for Selection. The

observed high mortality rates could result from hypoxia, cold, malnutrition, and other environmental factors associated with life at high altitudes. Consequently, there may be strong directional selection pressures in altiplano populations, for and against specific genotypes.

The following section will describe the growth patterns in high altitude populations that have been shaped by the joint influences of environmental and genetic factors.

Growth and Development in Andean Populations

Much of the data on growth patterns of the Andean populations at altitudes that range from 3000 m to 5500 m are provided by Frisancho (1978). Growth in stature and weight appears to continue until 22 years of age while growth in chest width and depth stops at about the age of 19. Sexual dimorphism in stature, weight, and chest size is not well defined until about the age of 16.

Interpopulation differences are exhibited by rural and urban groups and among populations at different altitudes. The urban groups exhibit heavier body weights than their rural counterparts; however, age for age, both groups attain nearly the same stature (Frisancho 1975). The higher-altitude groups, especially between the ages of 14 and 18, attained a significantly larger ($p < 0.01$) chest circumference at maximum inspiration than those residing at lower altitudes.

Compared with data derived from the U.S. (Stoudt et al. 1960) and with data on Peruvian samples from sea level and moderate altitude (Preto and Calderon 1947), Andean children at high altitude are absolutely and relatively smaller than their counterparts. However, they develop systematically greater chest circumferences, averaging about 8 to 10% above Americans and other lower-altitude counterparts. Thus the chest size of children at high altitude shows accelerated growth.

In females, subscapular skinfolds (a measure of trunk fat) steadily increase from childhood to adulthood but the triceps skinfolds (which measure limb fat) decline markedly after the age of 16 years. On the other hand, in males the increase in the subscapular skinfold thickness is very slow, while the triceps skinfolds decline substantially after the age of 10 and through adulthood.

Children residing at high altitude are markedly delayed in skeletal maturation for their chronological ages in comparison with U.S. norms. Peñaloza (1971) pointed out that the mean age at menarche among highland girls from Cerro de Pasco is 13.58 years, while at sea level it is 11.58 years. According to Llerena (1973), in ratings of secondary sexual maturation among high-altitude and sea level samples within the age range of 7 to 15 years, about 76% of

the boys at high altitude were in the prepubertal stage, while at sea level, only 39% were prepubertal. Consequently, the proportion of boys in the second, third, fourth, and fifth pubertal stages was lower at high altitude than at sea level. In the same manner, at sea level about 60% of the girls were already in the fourth pubertal stage, while at high altitude there were only 30% in this stage. In both males and females, then, the ages at which the secondary sexual characteristics are attained at high altitude are markedly delayed. Measurements of luteinizing hormones indicate that the adult values in girls are attained by the age of 11 at sea level and by 12 years at high altitude (Llerena 1973). According to the studies of Guerra-Garcia (1971), the excretion of urinary testosterone in adults is lower at high altitude than at sea level.

High-altitude boys show an accelerated growth in forced vital capacity (FVC) corresponding to the same rapid developmental pattern of the chest. Peruvian boys at high altitude, age for age, attain a significantly higher value than other Peruvians and U.S. sea-level norms (Frisancho 1975). The forced expiratory volume (FEV) and FVC, adjusted for height and weight, of the highland Quechuas are greater than those of their lowland Quechua counterparts (Boyce et al. 1974). Among the highland boys, the greater the chest circumference, the greater the FVC.

Development of the marrow cavity in bones proceeds at the same rate until the age of 12 years in both males and females, but sexual dimorphism in the marrow cavity is well defined after the age of 14 (Frisancho 1978). The differences in the pattern of growth in bone marrow between highlanders and lowlanders are probably related to the increased demand for functional activity. Studies on humans conducted by Merino and Reynafarje (1949) indicated that in the bone marrow, the ratio of nucleated red-cell elements to granulocytes in high altitude natives is 1:1, while at sea level, there is one nucleated red-cell element for every three granulocytes. These findings suggest that at high altitude the increased requirement for O_2 results in increased hematopoietic activity of bone marrow.

Objectives

The previous sections indicate that there are distinct phenotypic differences associated with high altitude in Andean populations, and *a priori* reasons for anticipating that some of the variations might have been shaped by genetic responses to life in such an extreme environment. The purpose of this study is to assess, for one Andean community, the proportion of additive genetic variance present in several traits under consideration: sitting height, bi-iliac diameter, acromial height, and biacromial diameter. The analysis of these traits will

complete the study of a set of twenty anthropometric traits that describe the thoracic and general bodily characteristics in a representative Andean population.

REVIEW OF PREVIOUS STUDIES

The mechanisms which determine the characteristic morphology seen in Andean populations remain unresolved. One view suggests that all differences between lowlanders and highlanders result from developmental changes of individuals exposed to an extreme environment characterized by appreciable hypoxia and cold. Another view, more logically a complement to the first rather than an alternative, is that such a harsh environment could allow natural selection to operate on populations having inhabited the South American altiplano for thousands of years, leading to the differentiation of high-altitude Andean populations. The following sections will review previous studies concerning the views mentioned above.

Studies Suggesting a Developmental Influence

Numerous studies attribute morphological differences between low and high altitude Andean populations a to developmental causation. Frisancho and Baker (1970) studied the physical growth of a high altitude Quechua population and suggested that the retarded pattern of physical growth of the indigenous population in Nuñoa was related to hypoxic effects of high altitude and/or reflected a genetic adaptation to environmental stress. Nutritional studies on animals indicate that increases in fat deposition speed maturation and dimensional growth (Hammond 1957). One dietary survey found that a relatively low protein and iron intake satisfies daily recommended allowances (Collazos et al. 1960, Picón-Reátegui 1978), suggesting that factors other than malnutrition or caloric deficiency (such as hypoxia inhibiting growth directly, or altering the frequencies of genes that shape growth patterns) could contribute to the slow and prolonged growth of populations such as the Nuñoa Quechua.

Measurements of skinfold thickness and upper arm circumference are good indicators of dietary sufficiency. Frisancho et al. (1975) compared the patterns of growth and body composition of 271 lowland Quechua children from Pamashto with those of 313 highland Quechua children from Ondores. The study indicated that lowland children tend to have less subcutaneous fat and arm muscle mass than do highland children. These authors explained the results by hypothesizing that during the last decade, the failure of the coffee crop in Pamashto

could have resulted in a marked deterioration of the economy. This economic pressure, in turn, is thought to have led to malnutrition especially influencing children, thus changing the pattern of body composition.

In their 1975 study, Frisancho et al. inferred highland and lowland similarities from ABO and Rh blood group frequencies. They concluded that morphological differences were not due to genetic differences, but instead were probably due to environmental stresses. However, it can be assumed that, although the two blood group loci show similar frequencies in the two populations, other loci could be influenced by causal factors different in both direction and magnitude. It is conceivable, for example, that selection could produce genotypically-based phenotypic differences in chest morphology or other anthropometric characteristics between the populations. This possible difference in relative selective pressure between loci influencing blood groups and loci influencing growth rates is very important, and might be open to empirical testing. Falconer (1960) demonstrated that, once a population that had been exposed to strong selective pressures was relieved of those pressures, the phenotypic response was usually in the direction opposite to that of selection. If the hypoxia at high altitude does indeed constitute a strong selective pressure, it is reasonable, in theory, to expect a reversal of the selective response in the lowland population. However, in practice it might be difficult or impossible to demonstrate such effects. There is also the possibility of a genotype-environment interaction taking place.

Mazess (1975) concluded from physiological studies that such organs as the heart, lungs, spleen, and liver, are large relative to the reduced body weight in high altitude populations. This is consistent with a reduction in cell number along with normal or large cell size; in contrast, malnutrition tends to produce a reduction in cell size but normal cell numbers (Naeye 1966). These findings seem to indicate that hypoxia has some direct effects on the activity of factors controlling cell division.

Lahiri et al. (1976) studied pulmonary responses to chronic hypoxia in order to clarify whether these adaptations were induced directly by exposure to a hypoxic environment, or whether they were attributable to genetic factors present only in high altitude residents. The populations they studied included Peruvian natives from Tacna (low altitude, 800 m), Puno (high altitude, 3850 m), and migrants to those cities from regions of contrasting altitudes. The investigators tested for the presence or absence of hyperventilation under simulated hypoxic conditions. Young migrants (less than 12 years old) showed a normal ventilatory response to acute hypoxia. From these findings, the authors postulated that diminished ventilatory response to hypoxia, and possibly also the increased lung volumes found in adult high altitude

natives, were determined environmentally rather than genetically. It was said that a genetic influence could be excluded since offspring of lowlanders born and bred at high altitude showed the same phenomena as native highlanders. However, their analysis neglected several important factors. First, the migrants from low to high altitude did not show a diminished response to hypoxia. Second, the sample populations being compared were of different genetic backgrounds, with different amounts of European admixture. Finally, the sample sizes were small; only 58 high-altitude natives (13 to 20 years old), and only 40 adult high-altitude natives were measured.

In his 1978 paper, Cruz-Coke suggested that it would have been difficult for Andeans to develop genes adaptive for living at high altitudes because they have not been present there for a long enough period of time. However, according to recent archaeological studies, the Andean plateau was peopled at least 11,000 years ago and quite possibly twice as long ago (MacNeish et al. 1970, Lynch and Kennedy 1970, MacNeish 1971, Vellard 1976). This period represents a minimum of 550 generations, clearly enough time for some genetic change to have occurred if there had been sufficiently strong selective pressure. Crow's (1958) Index of Opportunity for Selection has been used to demonstrate that the mortality component is much higher than the fertility component at high altitude (Garruto and Hoff 1976); overall, there has been ample opportunity for selection to have operated in high altitude Andean populations, but any effects of selection may be obscured by other complicating factors.

One study indicating the effect of cold temperature on body proportions at high altitude was carried out by Stinson and Frisancho (1978). The subjects were two Peruvian Quechua populations of reportedly similar genetic compositions, consisting of 242 lowland Quechua and 294 highland Quechua ranging in age from 7 to 19 years. The lowlanders resided in Pamashto which is characterized by hot-humid temperatures, whereas the highlanders who lived in Ondores were exposed to a cold and dry climate. The difference in body proportions found between the highland and lowland children are not due to nutritional differences alone (Stini 1972). Of the sample populations, the Ondores children are better nourished, being taller and having greater skinfold measurements than the Pamashto children (Frisancho et al. 1975). If the differences in body proportion between the two populations were due to nutritional differences, it might be expected that the better nourished highland children would have longer limbs relative to stature than their lowland counterparts. In fact, the opposite is true. The findings of this study are in accord with the theoretical expectation that populations living in cold climates would have shorter extremities than those living in warm climates. Shorter limbs and longer trunks would be adaptive to a cold environment in that they

would reduce the surface area available for heat loss (Riesenfeld 1973, Steegman 1975). Statistical analysis has confirmed this expectation on a worldwide basis (Roberts 1953). Overall, it is reasonable to conclude that the study by Stinson and Frisancho gives us more information about the complications involved in the search for altitude-related hypoxic effects than about the relative influence of genotype and a hypoxic environment on population differences.

Studies Suggesting a Genetic Causation

Development of the morphological characteristics of Andean populations may be influenced by genetic adaptation to high altitude through natural selection acting for a sufficiently long period of time. Though without direct proof, Hurtado (1932a, 1932b, 1971) said that the Andean native was not only under adaptive pressures throughout his lifetime, but also reflected genetic influences that have acted over many generations.

As noted above, archaeological studies by MacNeish (1971) have demonstrated a series of remains in the Ayacucho Valley of central Peru, which suggest continuous habitation of some highland areas from as much as 20,000 years ago to the present. This represents about 1000 generations, clearly enough time for selection to have occurred.

As noted earlier, Garruto and Hoff (1976) found that the mortality component (I_m) of Crow's Index of Opportunity for Selection (I) was much larger than the fertility component (I_f) for a high-altitude Quechua population. The values of I_m and I_f were 0.522 and 0.305, respectively; both values are consistent with potential for genetic change due to natural selection, particularly through differential mortality.

In a recent study of hematology and erythrocyte metabolism in Andean natives living at high altitude, Arnaud et al. (1985) compared Quechuas and Aymaras at a high altitude of 3600 m with the two populations at a low altitude of 450 m. The result indicated that for the Quechuas, the parameters concerning hematology and biochemistry are reversible under altered altitude conditions. In other words, biochemically and hematologically the Quechuas responded to high-altitude hypoxia as any lowlander did. However, the Aymaras showed enhanced adaptive characteristics: moderate polycythemia, hyperhemoglobinemia, microcytosis, metabolic hyperactivity with accumulation of ATP and 2,3-DPG, and methemoglobinemia with a drop in the activity of the methemoglobin reductase enzymes. After migration to the lowlands, even though the Aymaras showed decreased response to hypoxia, they still preserve some of those characters (methemoglobinemia excepted). The findings were explained by the authors as indicating that the Aymaras have peopled the more

isolated zone of the inter-Andean corridor, so that they are more homogeneous than the Quechuas who are descended from the great Inca culture which once predominated numerically, territorially, and socially (Vellard 1976). It is possible that these hematological and biochemical adaptive characters result from a response to selective pressure present at high altitude for numerous generations.

Beall et al. (1977) compared three Peruvian Quechua populations, consisting of low-altitude natives of low-altitude ancestry (Tambo I), low-altitude natives of high-altitude ancestry (Tambo II), and high-altitude natives of high-altitude ancestry (Nuñoa). They studied four morphological traits: stature, weight, anterior-posterior (A-P) diameter of the chest, and transverse diameter of the chest. The results showed that Tambo II was intermediate between Tambo I (taller) and Nuñoa (shorter); the relationship among the three populations was the same for the two chest dimensions. However, when the dimensions were plotted against stature, Nuñoa exceeded Tambo II which, in turn, surpassed Tambo I for transverse diameters. Similarly, Nuñoa residents exceeded those in Tambo I and II for A-P diameters. The authors concluded that these findings might be explained by two hypotheses. The first is that high-altitude hypoxia stimulates chest growth while it inhibits linear growth. The other is that chest growth is under a different genetic control than the development of stature and weight. These hypotheses are not mutually exclusive.

Quantitative studies leading to heritability estimates for anthropometric traits such as the ones studied by Beall et al. can give some evidence for genetic influences on variation. Eckhardt and collaborators (Kramer 1980 and this volume, Vandemark 1985 and this volume) have previously studied the proportion of genetic variance in twelve measurements that define the Andean thoracic morphology. Family analysis was used with data collected from 845 native highlanders resident in the village of Camacani in order to obtain heritability estimates for the traits. The midparent-offspring heritability estimate for sternal length in this high-altitude Peruvian population was 0.343, while that for sternal length in a sea level Belgian population was 0.787 (Susanne 1977). Although it would be highly desirable to have a broader basis of comparison from other low- and high-altitude populations, these values are consistent with the hypothesis that selection could have operated on sternal length at high altitude, not only increasing its mean length but also coincidentally reducing additive genetic variance. Worth noting in this regard is that increased sternal length is one of the most evident features of high altitude thoracic morphology.

The depth of the Andean chest can be analyzed by the standard IBP measurement referred to as the A-P diameter of the thorax. A midparent-offspring heritability estimate of

0.28 was derived for A-P diameter of the thorax in this high-altitude Peruvian population (Kramer 1980 and this volume). These and related findings demonstrated the existence of a genetic component in chest morphology, particularly in dimensions (such as chest length and chest depth) that contribute to the greater thoracic volume that would be advantageous at high altitude. It should be noted that those traits most directly associated with the thoracic complex showed lower heritability estimates, while those for overall body size showed higher heritabilities, as would be consistent with less influence from selection.

The midparent-offspring heritability estimate of stature this high-altitude Peruvian population was 0.509 (Kramer 1980 and this volume), which is consistent with comparable estimates from low-altitude populations. Stature was estimated to have a heritability of 0.65 in a West African population (Roberts et al. 1978). These two values from South American and Africa, respectively, are not significantly different when the standard errors of the heritability estimates are taken into account. The results indicate that in both populations stature shows moderately high heritability. Numerous other values consistent with the findings reported here are given by Mueller (1975).

The midparent-offspring heritability estimate for weight was 0.4003 with a standard error of 0.0656, and that for upper arm circumference was 0.4134 with a standard error of 0.0674 for the same high-altitude Peruvian population (Vandemark 1985 and this volume). In contrast, the midparent-offspring heritability estimate for weight was 0.625 in a sea level Belgian population and that for upper arm circumference was 0.458 (Susanne 1977). No standard errors of the estimates were reported for the Belgian study. The data on body size and composition can be interpreted in many ways, in part because skinfold and weight measures are labile to environmental influences such as diet and caloric expenditures. One simple observation is that for certain traits such as stature, there is fairly close agreement in values at high and low altitudes. Also worth noting is that, from the results obtained by heritability estimates for the anthropometric measurements noted here, there appears to be sufficient genetic variation on which natural selection can act to influence the anthropometric measurements in a high-altitude Peruvian population.

Conclusions Drawn from Previous Studies

From the brief review of previous work it is evident that complex environmental and genetic influences seem to be involved in development of the phenotypic features characteristic of high-altitude natives. To further elucidate these developmental features and their causes,

it is desirable to add quantitative genetic studies of other traits related to the thoracic complex.

MATERIALS AND METHODS

Estimation of Heritability

The estimation of heritability ($\hat{h}^2$) is commonly used in breeding programs. This statistic expresses the reliability of phenotypic values as a guide to the breeding value. The estimation can also help to assess the possibility of change in a quantitative character in response to selection, either artificial or natural. Heritability (h^2) is the population parameter that $\hat{h}^2$ estimates and can be defined in two ways as seen in Figure 1 below (Falconer 1983).

$$h^2_{broad} = V_g/V_p \qquad h^2_{narrow} = V_a/V_p$$
$$V_g = V_a + V_d + V_i$$
$$V_E = V_{Ew} + V_{Ec}$$
$$V_p = V_g + V_E$$

V_g=genotypic variance,V_a=additive variance,V_d=variance due to dominance deviations, V_i=variance due to epistatic interactions,V_E=environmental variance, V_{Ew}=variance within families, V_{Ec}=environmental covariance,V_p=phenotypic variance

Figure 1. Heritability Formulas

Heritability in the broad sense is the ratio of the genotypic variance to the phenotypic variance. The phenotypic variance is composed of two major components, the genotypic variance and the environmental variance. The genotypic variance can be subdivided further into three components: variance due to the additive effects of genes (breeding values), variance due to gene interactions at a single locus (dominance deviations), and variance due to interaction between loci (epistatic effects). The environmental variance is made up of two parts: environmental variance within a family and environmental covariance between families.

Compared with heritability in the broad sense, heritability in the narrow sense is more useful in a breeding program. The reason for heritability in the narrow sense being studied

is that the additive genetic variance reflects the influence on variation of genes that are passed from one generation to the next in the form of haploid gametes. As a result the variance due to dominance deviation or epistatic interaction is not transmitted.

It should be noted that the heritability of a character is specific for a certain population under certain environmental circumstances. All components of genotypic variance are influenced by gene frequencies, which can differ from one population to another and change from generation to generation in a natural population. The environments themselves can also vary among populations and through time. Therefore, the heritability estimate is, in theory, limited to a particular population at a specific time.

The estimation of heritability is based on the resemblance between different sorts of relatives. Table 1 shows the methods most commonly used to estimate heritability. Regression coefficients are computed in offspring-parent analysis. Intraclass correlations are calculated in sib analysis.

Table 1. Methods of Estimating Heritability

Relationship	Proportion of the Variances that the Covariance Measures V_i						Regression b; Intraclass Correlation t $\hat{h}^2$
	V_a	V_d	V_{aa}	V_{ad}	V_{dd}	V_{Ec}	
Single Parent-Offspring	1/2	—	1/4	—	—	—	2b
Midparent-Offspring	1/2	—	1/4	—	—	—	b*
Sib Analysis	1/2	1/4	1/4	1/8	1/16	1	2t
Half-Sib Analysis	1/4	—	1/16	—	—	—	4t

*since V_p is also halved

Each method has its advantages and disadvantages. Half-siblings are uncommon in many human populations so that the method of half-sib analysis is usually impractical. In sib analysis, the correlation is the least reliable method because the estimate for heritability contains variance due to dominance deviation. The environmental covariance term (Ec) is also larger in full sib analysis than in parent-offspring analysis. Since the environmental

covariance is less in father-offspring pairs than in mother-offspring pairs, the former method is sometimes preferred for estimating heritability (Falconer 1983).

If there is assortative mating, the method of midparent-offspring analysis is recommended (Falconer 1983). Assortative mating gives rise to an increase in the variance of midparent values, leading to a lower standard error and, in turn, to a more precise estimation of heritability. Because of these and other considerations, the choice of a method for determining the heritability of a trait depends on the population under study.

There are two factors of major importance in the estimation of heritability. One is the minimization of Ec, which is accomplished by the selection of the correct method. The other is related to the standard error. Because $\hat{h}^2$ is a statistic, it has a sampling error which in part determines the precision of the estimate. To attain a standard error of 0.15 or less, 200 parent-offspring pairs or 150 midparent-offspring pairs are needed (Falconer 1963).

These underlying matters have been considered as part of our attempt to calculate the most accurate heritability estimates during an ongoing study that has been conducted to assess the extent to which genetic factors have shaped variation in measurements of chest and overall body size in a high-altitude Peruvian population. The following paragraphs of this section will describe the population and measurements taken. The subsequent section will describe the methods used to calculate heritability estimates.

Procedures of the Experiment

Camacani is a small village situated on the shore of Lake Titicaca at an altitude of about 3900 m in the Department of Puno, Peru. It has approximately 2100 inhabitants, chiefly of Aymara descent. In 1978 a field study was conducted by Dr. Robert B. Eckhardt in this village in order to evaluate the relative contributions of environmental variation and genetic variation to thoracic morphology in a native high-altitude Andean population. Inhabitants of the village are primarily engaged in agriculture, producing crops for subsistence and local markets. Most older adults have had relatively little formal schooling but the educational levels are increasing steadily among younger generations.

Children answered a questionnaire which documented sex, age, place of birth, and place of residence. Adults responded to a more lengthy survey which asked not only age, sex, place of birth, and place of residence, but also included 9 socioeconomic questions to assess the extent of environmental homogeneity, along with a list of offspring and other relatives. Adults were also administered a general health survey designed to evaluate the overall condition of the respondent with a special focus on cardiovascular fitness. A set of 20 anthropometric

measurements was then taken on both children and adults in order to describe thoracic morphology and nutritional status.

A total of 845 people were measured, chiefly structured within family groups. The few subjects who had lived at lower altitudes were subsequently excluded from the data analysis. The final sample size in this study comprised 811 subjects, including 369 adults and 442 children (from several months to 19 years). From these data it was possible to identify 264 midparent-offspring pairs, 324 father-offspring pairs, and 369 mother-offspring pairs. These numbers of parent-offspring pairs made it possible to satisfy the minimum goal of obtaining a standard error of the heritability estimates of 0.15 or less.

This study will focus on the heritability estimates of four anthropometric measurements: sitting height (which combines the lengths of the trunk, neck, and head), bi-iliac diameter (breadth across the hips), acromial height (comprising trunk length alone), and biacromial diameter (breadth across the shoulders). Heritability estimates for sixteen other anthropometric measurements have been calculated previously (Kramer 1980 and this volume, Vandemark 1985 and this volume). Measurements were taken with an anthropometer following procedures prescribed by the International Biological Programme (IBP) handbook (Weiner and Lourie 1969).

Statistical Analysis

Heritability estimates were made on the two International Biological Programme (IBP) body size measurements and two IBP chest measurements. The midparent-offspring analysis was used as a primary method in this study (Falconer 1983). Father-offspring regression could underestimate h^2 for several reasons, including any illegitimacy that might occur in the population. Mother-offspring regression, on the other hand, could overestimate heritabilities due to the presence of maternal effects. Consequently, it is reasonable to conclude that the midparent-offspring analysis is likely to be more accurate than the alternative methods. A further consideration regarding the accuracy of different estimates is that the standard error of the heritability estimate is the same as that of the regression coefficient in the midparent-offspring analysis while the standard error of the heritability estimate derived from one parent-offspring analysis is twice the standard error of the regression coefficient. Thus the midparent-offspring regression may contribute a more reliable heritability estimate for the traits concerned, by offsetting the possible sources of bias present in the one parent-offspring analysis, while avoiding inflation of the error term. Father-offspring and mother-offspring heritability estimates were also calculated, however.

Comparison of these two estimates can indicate the extent to which illegitimacy or maternal effects are present in the population (Falconer 1983).

Heritability estimates on full sib intra-class correlations were also calculated regardless of the fact that the estimates include dominance deviations and environmental variations. The extent of nonadditive genetic variance can be estimated by comparison of the midparent-offspring heritabilities with those arising from full sib intraclass correlations (Falconer 1983).

A problem in the computation of the regression coefficient occurs in families with unequal numbers of offspring. One method to handle this imbalance is to count the parental values as many times as there are offspring. However, this method would give a heavy weight to certain parents with many offspring. Another alternative to circumvent the problem would be to pair each parental value with the average of offspring values in that family. However, in this latter approach offspring in larger families would be under weighted. In order to make the best use of all the data, it is desirable to combine the sums of squares and products from families of a particular size according to a weighting factor determined by the family size. Families of various sizes are weighted in proportion to the reciprocal of the variance of the estimate of regression resulting from families all of that particular size.

The derivation of the weighting factor can be found in Falconer (1963). The first step in computing the weighting factor is to calculate the phenotypic intra-class correlation, t, from the analysis of variance. The next step is to estimate the unweighted regression coefficient, b, of the unweighted offspring means on the parental values. With estimates of the correlation, t, and the regression, b, the weighting factor can be computed in two steps. First the quantity T must be obtained as follows: when regression is made on a single parent

$$T = (t - b^2)/(1 - t),$$

and when the regression is on the mean of both parents

$$T = (t - \frac{1}{2}b^2)/(1 - t).$$

Then the weighting factor, Wn, corresponding to families of n offspring is

$$Wn = (n + nT)/(1 + nT).$$

A Pascal program to perform these calculations had been developed (Vandemark et al. 1985).

Another problem in data analysis arises when the subjects in the sample are of different ages and sexes. One method of surmounting this problem would have been to separate the sexes for both parents and offspring, then to have used growth curves to adjust all offspring measurements to a single age. One drawback of this approach is a reduction of the data, and another arises from the uneven growth curves that are due to variations in growth among populations. An alternative method is to make age and sex independent variables along with the offspring value, and then to calculate multiple regression equations. However, this approach introduces two additional error terms into the model since both age and sex have their own beta coefficient distributions.

A more efficient approach to the problem of a heterogeneous sample is age-sex standardization of all measurements. In this study, each individual's raw values were converted into z-score deviations from the mean of the specific parameter for a particular age and sex class. This approach introduces only one additional error term into the model and also has several advantages. Standardization corrects inequality of variances between sexes. In addition it removes differences between cohorts, consequently allowing comparison of offspring of various ages.

Finally, the standard error of the heritability estimates should be considered. The magnitude of the standard error indicates the degree of precision of the heritability estimate. The magnitude of the standard error of the heritability estimate is related to the regression coefficient or the intra-class correlation (Falconer 1963). In a midparent-offspring regression, the standard error of the heritability estimate corresponds to that of the regression coefficient while in a one parent-offspring regression the former is equal to twice the latter. In a full sib analysis the standard error of the heritability estimate is twice that of the intraclass correlation. As noted earlier, calculations were performed using the program developed by Vandemark et al. (1985).

RESULTS

Midparent Heritability Estimates

In order to estimate the heritabilities for the traits under study, the regressions of offspring values on midparent values were computed using the weighted method discussed above. The heritability estimates were derived from the resulting regression coefficients.

These are listed in Table 2 in order of declining rank order of the heritability values: bi-iliac diameter, sitting height, acromial height, and biacromial diameter. The standard errors of the estimates are also shown in Table 2.

Table 2. Heritability Estimates on Midparent-Offspring Regressions

Trait	$\hat{h}^2$	Standard Error
Bi-iliac diameter	0.3883	0.0620
Sitting height	0.3368	0.0699
Biacromial Diameter	0.1489	0.0692
Acromial height	0.1184	0.0590

Bi-iliac diameter has a moderate heritability estimate of 0.3883 ± 0.0620, and sitting height has a fairly similar estimated value of 0.3368 ± 0.0699. The heritability estimates for biacromial diameter and acromial height are lower, 0.1489 ± 0.0692 and 0.1184 ± 0.0590, respectively.

In all cases, the standard errors of the heritability estimates are modest, ranging from approximately 0.059 to 0.070. From these values it appears that the sample population was sufficiently large to make it possible to obtain reasonably precise heritability estimates.

One Parent-Offspring Heritabilities

Heritability estimates along with standard errors were also obtained by father-offspring and mother-offspring regressions. These are given in Table 3 where they are compared with midparent heritability estimates. The traits are again listed in rank order of midparent heritability estimates. All traits except bi-iliac diameter show higher maternal estimates than paternal or midparent estimates, and even the paternal value for bi-iliac diameter is only slightly higher than that for the maternal or midparent estimate. It seems highly probable that maternal effects might be operating in these traits, though the magnitude of any maternal effect is not great.

The midparent estimate is between the paternal and maternal estimates for both bi-iliac diameter and sitting height. In the case of sitting height, the paternal estimate, as expected, is lowest.

Table 3. Mother-Offspring and Father-Offspring Heritability Estimates
Compared With Midparent-Offspring Estimates

Trait	Mother-Offspring $\hat{h}^2 \pm$ S.E.	Father-Offspring $\hat{h}^2 \pm$ S.E.	Midparent-Offspring $\hat{h}^2$
Bi-iliac diameter	0.4185±0.0965	0.4475±0.0809	0.3883
Sitting height	0.4068±0.0942	0.2766±0.0881	0.3368
Biacromial diameter	0.2880±0.0967	0.1604±0.0918	0.1489
Acromial height	0.2336±0.0912	0.1783±0.0841	0.1184

In the remaining two traits, the paternal estimate is, in magnitude, between the maternal and midparent estimates. Once again, the differences are not very great, either absolutely or in proportion to the error terms estimated. Another factor potentially contributing to the discrepancy is that the sample of midparent-offspring pairs is smaller in size than that of both mother-offspring and father-offspring pairs by about 80 to 100 pairs.

The standard errors of the mother-offspring heritability estimates range from 0.091 to 0.097, while the corresponding standard errors of the father-offspring heritability estimates vary between 0.081 and 0.092. These standard errors satisfy reasonable expectations for precision.

Comparison of Sib Analysis Heritabilities with Those Based on Other Relationships

Even though a heritability estimate from sib analysis will have components of nonadditive genetic variance, it can be a valuable addition to a study of this sort because of its potential for giving an indication of the effects of nonadditive genetic variance and common environmental variance on the trait in question when compared with the heritability estimates from alternative methods. Table 4 shows the heritability estimates based on sib intra-class correlations for the four traits studied along with maternal and midparent estimates for comparative purposes.

For bi-iliac diameter the maternal estimate is higher than the midparent estimate, which is, in turn, greater than the sib estimate. This is consistent with an interpretation that

the trait is influenced mainly by the maternal effects but by little or no nonadditive genetic variance.

In the instances of sitting height and biacromial diameter, the maternal estimate is largest, followed by the sib estimate, and the midparent estimate is lowest in magnitude. This indicates that some maternal effects may exist for these traits as well as some nonadditive genetic variance.

Table 4. Heritability Estimates Derived From Sib Analysis With Comparative Estimates

Trait	Sib Analysis $\hat{h}^2 \pm$ S.E.	Maternal-Offspring $\hat{h}^2$	Midparent-Offspring $\hat{h}^2$
Bi-iliac diameter	0.3527 ± 0.1154	0.4185	0.3883
Sitting height	0.3947 ± 0.1119	0.4068	0.3368
Biacromial diameter	0.2798 ± 0.1126	0.2880	0.1489
Acromial height	0.3995 ± 0.1125	0.2336	0.1184

Acromial height has a sib estimate which is greater than the maternal estimate, which is, in turn, greater than the midparent estimate. These values imply the existence of some nonadditive genetic variance stronger than whatever maternal effects are present in the trait. However, the higher sib estimate could be due to other factors of the common environment besides maternal effects.

The standard errors of the heritability estimates derived from sib analysis fall between 0.112 and 0.115, higher than the error terms derived from parent-offspring regressions, but still within the bounds of acceptability.

One final factor which should be borne in mind when interpreting the estimates for each trait derived from the various relationships is the cumulative overlap inherent in the error terms. Although real maternal and nonadditive effects may be present as suggested above, the most conservative interpretation simply would be to conclude that all the traits examined here have moderately low heritabilities, and that differences derived from one estimation technique versus another could merely reflect unavoidable experimental error.

DISCUSSION

Credibility of the Heritability Estimates

Genetic studies of human populations are carried out under many restrictions which might not be found in studies of plants or animals. For example, ignorance of an illegitimate birth in a human population makes a pedigree incorrect. In addition, one generation in a human population is longer than in other experimental subjects so it may be difficult to collect enough data to attain accurate results from a study. For these technical reasons, as well as numerous theoretical considerations, the validity of the resulting estimates from a human quantitative genetic study should be carefully examined.

In this study, one of the goals of the experiment was to obtain acceptably low standard errors of the heritability estimates. All the heritability estimates have their standard errors in the range of 0.059 to 0.115, achieving the above goal, and implying that sufficient data have been obtained in order to make reasonably precise heritability estimates.

It was expected that the maternal estimate would be greater than the midparent estimate which, in turn, would be larger than the paternal estimate. This was the case for only one of the four traits. However, the other discrepancies were slight and within the bounds of experimental error. These results may reflect differences in sample sizes among the three methods. Even considering these complications, the resulting heritability estimates seem to be reasonable in the context of other traits studied in this population and in other human populations.

Interpretations Arising from the Heritability Estimates

Of the four traits analyzed, bi-iliac diameter has the highest heritability estimate based on the midparent-offspring regression, with high estimates derived from alternative methods. The inflated paternal estimate for this trait may be due to sampling deviations or a characteristic of this trait which influences resemblance between father and offspring.

For sitting height, the maternal estimate is slightly higher than the sib estimate, and both exceed the midparent estimate. This pattern suggests that maternal effects may operate more strongly in the traits than other environmental deviations or nonadditive genetic variations.

The result derived from biacromial diameter measurements has the lowest midparent estimate in comparison with those based on other analyses. This result reflects considerable maternal influence which can theoretically include nuclear, cytoplasmic, or environmental effects, singly or in combination (Nance et al. 1978).

Acromial height has a sib estimate which is higher than other estimates. Nonadditive genetic variance may contribute to the development of this trait. Therefore maternal effects and nonadditive genetic variations, which are difficult to distinguish from the additive gene effects, seem to be present in the traits analyzed.

Extension of the Results

The purpose of this study was to estimate heritabilities in order to determine the amount of additive genetic variation in the traits describing the morphology of the thorax and overall body in one Andean population.

The magnitudes of the computed heritability estimates varied among the four traits under study. Bi-iliac diameter and sitting height had moderate heritability estimates, while acromial height and biacromial diameter had somewhat lower heritabilities. The results from the study could be interpreted in several ways. First of all, the low heritability estimates for the chest traits imply the possibility of more substantial environmental influence on variation in the chest traits than on variation in traits indicating body size. For example, Kramer (1980 and this volume) computed heritability estimates for several other traits which help define the thorax in Andean populations. Anterior-posterior diameter of the thorax had a relatively low heritability estimate of 0.280. For transverse diameter of the thorax the estimate was 0.145 and for thoracic circumference it was 0.157. However, stature had a higher heritability estimate of 0.509 (Kramer 1980 and this volume). Nonadditive genetic effects or environmental influences may have contributed to the differential estimates between the chest traits and the traits of body size.

The low heritability estimates obtained for the thoracic traits in this study and previous studies using the same data set could, however, reflect the operation of differential selection for chest and body size over past generations. It was noted earlier that the Andean thorax was large relative to stature. Such allometric differences could result from selection operating more strongly on chest dimensions than on stature. It could explain the relatively low heritability estimates for thoracic traits since directional selection for large chest volume would reduce additive genetic variation as it shifted the population means for these traits.

Other evidence could be adduced for natural selection operating in high-altitude Peruvian populations. Eckhardt and Dutt (1979) compared morphological differences in the chest between high- and low-altitude Andean populations. The thoracic volume was changed by over 20% in a time interval of 20,000 to 10,000 years at high altitude. This fast rate of possible evolutionary change could be due to the influence of natural selection on the trait. The time interval is sufficient for selection to have operated over hundreds of generations in populations confronted with harsh environmental conditions (Eckhardt 1985).

When compared with heritability estimates for body weight in sea level populations, the volume was lower in this Andean population (Vandemark 1985 and this volume). Although Roberts (1953) noted that increases in body weight are proportional to decreases in temperature, in high-altitude Peruvian populations reduced body weight is a common finding in spite of the cold environment. Such results suggest that, in high altitude Andean groups, growth may occur in an environmental setting which simultaneously imposes stresses (such as hypoxia) which increase chest size even as general body growth is constrained, as by limited caloric intake and cold stress, which would increase caloric expenditures. This combination of factors could produce selection for different growth rates in different components of body size, as seems to be the case in this study population.

The distinctions in morphology between high and low altitude Andean populations, along with the structure of heritability estimates found in this and associated studies, could be regarded as consistent with a hypothesis of evolutionary change taking place in a human population long exposed to an extreme environment.

CONCLUSIONS

Heritability estimates were made on four anthropometric traits in a high-altitude Andean population in order to assess the amount of genetic variation present in these traits. For chest traits the heritability estimates varied, but were low to moderate overall. From these results, and those of previous studies, it was postulated that although a significant component of environmental variance seems to be involved in adaptation to a high-altitude environment, there is also non-trivial genetic variance.

CHAPTER 7

MEASUREMENT OF NATURAL SELECTION ON CORRELATED ANTHROPOMETRIC
CHARACTERS IN A HIGH ALTITUDE ANDEAN POPULATION

Young Im Ahn

ABSTRACT

Numerous studies have demonstrated that Andean populations at high altitudes exhibit a slow pattern of physical growth resulting in short stature combined with high thoracic volumes. Such developmental and morphological characteristics may reflect in part genetic adaptation to environmental stresses introduced by high altitude. The objective of this study is to test the general hypothesis that natural selection has operated with differential degrees of magnitude on anthropometric characters related to altitude adaptation in an Aymara population resident at an altitude of about 3,900 m.

The population sample comprises 807 subjects on whom a set of 20 anthropometric measurements was taken. These measurements describe overall body size, thoracic morphology and nutritional status. The approach we used was pioneered by Pearson (1903) and modified by Lande and Arnold (1983) to measure selection from observed changes in the distribution of phenotypic characters between two generations. Anthropometric measurements were standardized, frequency distributions were checked for normality, and any traits that did not show normality were adjusted by log transformation. Genetic and phenotypic correlation matrices were calculated for 20 anthropometric traits. Since high correlations depart from an underlying assumption of this selection model and also may conceal the true effect of selection on a trait, the character set was reduced to eight traits reflecting body size and thoracic dimensions, which can represent this high-altitude population: stature (HT), sternal length (STL), acromial height (AH), anterior-posterior thoracic diameter (APT), anterior-posterior thoracic diameter at manubrium (APM), transverse chest diameter (TD), biacromial diameter (BD), and bi-iliac diameter (BID).

The results showed that there is broad similarity between the genetic and phenotypic correlation matrices, indicating that genetic and environmental effects on development typically produce similar patterns of phenotypic variation. Standardized selection gradients

obtained were APM(0.876), APT(0.574), AH(-0.504), BID(-0.426), STL(0.393), BD(0.318), TD(0.199), and HT(-0.160). Overall, in this population natural selection has operated more strongly on thoracic dimensions related to chest depth and length, and less strongly on dimensions related to general body size such as stature. A larger volume of the chest, along with reduced stature, appears to be selected for at high altitudes.

INTRODUCTION

DEFINITION OF NATURAL SELECTION

In his book, The Origin of Species in 1859, Darwin developed his ideas about evolution by natural selection based on observations of phenotypic variation. Darwin's theory of natural selection was that in every generation the numerous members of each species compete for survival and the ones with the most advantageous phenotypic characteristics survive and perpetuate their kind. Despite many important additions and qualifications through the period of over a century since Darwin's formulation, natural selection remains a key component in our understanding of the evolutionary process.

Natural selection can be defined as a process of evolution based upon three premises: variation, fitness differences and inheritance (Endler 1986). Natural selection can take place if a trait in a population shows variation among individuals, and if certain phenotypes of that trait are more adapted to their environment than are other phenotypes, by virtue of their greater ability to survive and reproduce in that environment. In addition, natural selection can occur if, in the population, there is biological transmission of that trait from one generation to the next. These three conditions are necessary for the process of natural selection to take place. A common result is that phenotypes with greater fitness values leave, on the average, more offspring than do phenotypes with lower fitness values. Consequently, the trait distribution in the offspring generation predictably will be different from that of the parental generation so as to promote greater adaptation to the environment.

PREVIOUS STUDIES OF SELECTION IN NATURAL POPULATIONS

Examples of Natural Selection on Qualitative Traits

It is important to note that natural selection is the main driving force of evolution, the process that leads to improved adaptation of populations to their environments. Natural

selection acts on phenotypes, not on genotypes, and it acts on the whole phenotype as it is determined by many loci and numerous environmental factors.

Natural selection occurs when differences in some phenotypic characteristics result in consistent differences, on average, in rate of survival or reproduction. When such phenotypic differences are correlated with survival or reproduction, natural selection can operate; however, there will be no evolutionary response to selection unless the phenotypic differences are, at least partly, due to genetic differences.

There are three major modes of selection, depending on the relationship between phenotypes and fitness. If the relationship is monotonic, so that an extreme phenotype is the most fit, selection is directional. If intermediate phenotypes are the most fit, selection is stabilizing. If two or more extreme phenotypes have high fitness, but intermediates between them have low fitness, selection is disruptive.

Industrial melanism in moths is perhaps the best described case of directional selection at a single locus in natural populations. The black morph of the moth Biston betularia increased in frequency from 1 percent to more than 90 percent in some areas within less than a century after onset of the Industrial Revolution in England. Kettlewell (1973) showed that the morphs differ greatly in susceptibility to predation by birds, which represent an important source of selection. The first evidence for the adaptive importance of camouflage is that the color morphs preferentially rest on backgrounds that make them least conspicuous. Second, in a mark-recapture experiment, the proportion of melanics recovered is about twice as great as that of nonmelanics in a polluted area. Third, direct observations of predation by redstarts in light and dark areas showed that in dark areas proportionally more nonmelanics were eaten, and in light areas proportionally more melanics were eaten. Hartl and Clark (1989) discussed a number of complications in industrial melanism. First, there are genetic complexities. While the key cause of melanism in Biston betularia is a single dominant allele, in certain areas moths neither light nor dark but of intermediate shades of grey are found. This intermediate coloration seems to be due to alleles at the same locus, but other loci also may be involved. There are also complications in the selective forces. Although bird predation is undoubtedly an important source of selection, there seem to be differences in viability between color morphs. Considering the intensity of selection involved, furthermore, it is notable that there is no fixation of the allele for melanism. Another complication in the mating system is that the color morphs may be under a degree of negative assortative mating. Despite these complications, the evolution of industrial melanism in Biston betularia and a number of other species of moths remains a classic example of rapid evolutionary change in response to human alteration of the

environment (Bishop and Cook 1981). There are numerous other examples that are not as well known. Populations of hundreds of species of insects have evolved resistance to various insecticides (Wood 1981). Some plants have become resistant to toxic heavy metals in the vicinity of mines (Antonovics et al. 1971), and many species of weeds have developed resistance to herbicides.

One of the few well-documented cases of heterozygote superiority at a single locus is that of sickle-cell hemoglobin in humans. Hemoglobin S differs from its normal counterpart, hemoglobin A, by a single amino acid. The beta polypeptide chain of hemoglobin A is a sequence of 146 amino acids with glutamic acid in position 6. In hemoglobin S, glutamic acid in position 6 is replaced by valine. Hemoglobin S forms large crystal aggregates under conditions of low oxygen tension. The aggregation is the result of a tendency of that end of the beta chain near position 6 to form a ring of amino acids in the presence of valine in that position. These rings result in an interlocking of adjacent hemoglobin molecules, which leads in turn to the formation of the crystalline aggregates. People who are heterozygous for the S allele can suffer from serious anemia (sickle-cell trait), but in parts of Africa where malaria is prevalent, their survival rate is higher than that of homozygotes for the more common A allele. Haldane (1949) suggested that the maintenance of the sickle-cell polymorphism was due to the heterozygote AS conferring an advantage in malarial areas. Much evidence shows that the heterozygote for the sickle-cell gene is at advantage over both homozygotes and that this advantage is due to increased resistance to malaria. In parts of West Africa, the expected frequency of the S allele, according to this model, is about 0.13, which is close to the frequency actually observed (Allison 1961, Cavalli-Sforza and Bodmer 1971). Several other hemoglobin variants, such as the hemoglobin C allele and thalassemia, also appear to show heterozygous advantage in human populations under malarial conditions.

The blood-cell antigens provide other outstanding examples of polymorphism in human populations. Some blood-group and other polymorphisms detected by immunological techniques are potentially subject to a special type of selection by incompatibility. This is the consequence of reactions between maternal antibodies and fetal antigens as the result of immunological differences. The fetus may thus be selected against.

Apparent heterozygous advantage has been described for a number of other polymorphic genes, such as a color polymorphism in the copepod Tisbe reticulata (Battaglia 1958). Also, Drosophila pseudoobscura that are heterozygous for chromosome inversions sometimes display higher viability, fecundity, or mating ability than chromosome homozygotes (Dobzhansky 1970).

Examples of Natural Selection on Quantitative Traits

In a classic study of selection on quantitative characters, Bumpus (1899) collected 136 English house sparrows (Passer domesticus) on February 1, 1898, after a severe snowstorm and measured nine characters on the birds. Out of the sample, 72 survived and the rest died. They were also classified by sexes and the males into young and adults. The Bumpus data have been analyzed several times later by different authors (Johnston et al. 1972, O'Donald 1973, Lande and Arnold 1983). It has been found that the selection imposed on the sparrows by the storm must have been in favor of an optimum total wing length considerably shorter than the average but favoring an optimal length of humerus near the mean value.

Boag and Grant (1981) studied a population of the Galapagos finch, Geospiza fortis, that suffered a severe decline during an intense drought. When the food supply was reduced, the survivors turned to seeds larger than the species usually fed on. Apparently large birds had greater access to the seeds, or a greater ability to feed on them. Since the heritability of size in this population is 0.76, a considerable evolutionary increase in size would occur if the harsh environmental conditions were to persist. This example illustrates that directional selection can be stringent under natural conditions, and that rapid evolution in morphological features can be documented in vertebrate populations.

Arnold (1987) examined the microevolution of vertebral numbers in garter snakes, using coastal and inland populations of the garter snake Thamnophis elegans in California. In both populations, the two traits studied (number of body vertebrae and number of tail vertebrae) are highly heritable but show only a weak, positive genetic correlation. The net forces of directional selection were computed to account for the observed divergence in means. The results indicated that selection on the body was three times stronger than selection on tail length. Despite the weak genetic relationship between the two traits, correlated responses to selection on the body apparently played a major role in the microevolution of tail vertebral number.

Stabilizing selection keeps the population mean at some intermediate value. Perhaps the most clear-cut example of a character subject to stabilizing selection is birth weight in humans. Infants with intermediate weight at birth have the highest survival rate (Karn and Penrose 1951). Karn and Penrose estimated that for babies weighing between about 5.9 pounds and 10 pounds at birth, the mortality rate is less than average while for those outside these limits it is greater than average. Very similar results have been obtained by other workers with data from widely differing human populations. Among other species, Hecht (1952) found that in lizards of genus Aristelliger, the mean body size was determined by the balance between the advantage that larger lizards have in defending territories and the disadvantage

that they suffer in being more susceptible to predation by owls. In ducks (Anas platyrhynchos; Rendel 1943) and chickens (Gallus gallus; Lerner and Gunns 1952), eggs of intermediate weight have the highest hatching success.

Disruptive selection has been less extensively studied in natural populations than directional and stabilizing selection. It may be quite common, however, under conditions where different phenotypes in a resource-limited population are specialized for different resources. For example, selection favors multiple discrete phenotypes in the swallowtail butterfly Papilio dardanus in southern Africa (Clarke and Sheppard 1960, Ford 1975). Some females of this butterfly have black wings with white patches, some have the white patches reduced to small spots, and others have extensive reddish-brown areas on the wings. The color pattern is stabilized by polygenic modifier loci, the effects of which become evident when these females are crossed with a nonmimetic race from Madagascar. Various intermediates among the mimetic form then appear among the progeny. These results indicate that in South African populations, selection has favored modifier genes that restrict the expression of the major genes to one of several discrete alternative phenotypes.

In a study of the maintenance of genetic variability in heterogeneous environments, Brodie (1989) reports the existence of genetic correlations between morphology and antipredator behaviour in natural populations of the garter snake (Thamnophis ordinoides) in coastal Oregon. He demonstrates that selection favouring particular combinations of color pattern and behaviour may be at least partially responsible for the maintenance of genetic covariances. This study indicates that the phenotypic changes in morphology and behavior will be a result not only of direct selection on those characters, but also of indirect selection on genetically correlated characters.

ADAPTATION IN HUMAN POPULATIONS

Natural selection is the only force capable of bringing about the long-term adaptation of a population to the environment. Consequently, it is reasonable to expect that this force of evolution has been instrumental in shaping genetically based characteristics of our own species. Most environments impose several different stresses on the human populations that inhabit them, and these populations have numerous alternative and overlapping mechanisms for responding to the challenges. Among these mechanisms, genetic adaptation alone produces permanent change in the gene pool from generation to generation.

As a classic example of human genetic adaptation to climate, it has been shown that dark skin color provides a selective advantage in the tropics. In this instance there are several

explanations of how natural selection takes place (Cavalli-Sforza and Bodmer 1971). One possible explanation is that light-skinned people, especially children, exposed to the sun in the tropics are at high risk due to erythematous reactions and this is the basis for selective response. However, in several African populations albinos survive, and their frequency is perhaps not too different from that in white populations. Thus, a more extreme lack of pigmentation than that found in the ordinary person of European ancestry does not seem to be very dangerous even in the tropics. The second explanation may be that dark skin affords protection against skin tumors. According to the known frequency of such tumors today, it hardly seems important enough to account for a selective effect. The third possible alternative is that the selective factor may be vitamin D deficiency or excess. A dark skin would prevent the formation of excessive amounts of vitamin D, which could be dangerous, in areas with intense sunlight (Livingstone 1969). A light skin, however, would allow the formation of excessive amounts of this vitamin in these areas. All of these mechanisms, and others, may have participated in the process of skin color change, but as yet it is very difficult to assess their relative importance.

Another example is genetic adaptation to cold in humans. Schreider (1964) has studied the body weight-to-surface ratio, which is expected to be higher in areas having a cold climate and lower in those having a hot climate. In Europe, the ratio, in units of kilograms per square meter, goes from 39 in Germany or Finland to 37 in Calabria, Southern Italy. The picture is somewhat different for Africans, who show an approximate gradient with temperature ranging from 37 in Mali to between 30 and 31 among Bushman and Pygmies. Among populations of the Pacific, or among inhabitants of cold countries (such as Eskimos or Mapuches of the Andes) the ratio is higher (38 to 39 and 39.2, respectively). Hotter countries give lower figures: for example, 31 to 32 for the Phillippines and 30.9 for Malaya. It should be noted, however, that the rule on the variation of body weight-to-surface with temperature seems to hold for men, not for women. This may reflect the tendency toward division of labor between men and women, with men being more exposed to conditions of extreme stress, in which case selection due to climatic conditions may be more important.

Another example of adaptation is the variation in the ratio of the length of the limbs to that of the trunk. The greater the ratio, the greater the loss of heat. The ratio is therefore expected to be lower in colder climates and higher in hotter ones. It is found to be lowest in Northern Europe and highest in Pygmies, with a fairly regular gradient in between.

Steegman (1975) also found that many human populations living in cold areas have higher body weights, larger chests, and shorter extremities. Genetic and environmental

influences on developmental processes can combine to produce these features. Physiological responses to cooling of the extremities differ among populations from major geographic areas of the world. Steegman inferred that under cold stress the African ancestors of blacks simply retained a tropical pattern of heat conservation. In contrast, Europeans evolved in areas where exposure to severe cold was a common occurrence, and adaptations to such conditions were evolved and retained. Adult natives of Asian origin, such as Eskimos and American Indians, have shown a cold response superior to that of Europeans. Therefore, the differential responses to cold stress among human populations may have at least a partial genetic basis.

Numerous studies have been carried out on human adaptation to high altitude (Baker 1969, Clegg et al., 1970, Frisancho and Baker 1970, Mazess 1975, Frisancho 1976 and 1978, Beall et al. 1977). These studies generally demonstrated that human populations at high altitude in the Andes have a slow pattern of physical growth overall, combined with high thoracic volumes. The developmental and morphological characteristics seen in high altitude populations may reflect in part a genetic adaptation to environmental stress such as hypoxia.

In the study of hematology and erythrocyte metabolism, Arnaud et al. (1985) studied several South American Indian groups of different size and linguistic affinity. In particular, high-altitude populations of Quechua and Aymara speakers were compared with their counterparts at low altitude. The results indicated that the Quechua responded to high-altitude hypoxia biochemically and hematologically as any lowlanders did. However, after migration to the lowlands, the Aymara of high altitude ancestry still maintained some distinctive highland biochemical and hematological characters. The different findings for the Quechua and the Aymara populations were thought to reflect population history. The Aymara population is believed to have peopled a more isolated, highland region, and their hematological and biochemical adaptive characters may have resulted from response to selective pressures present at high altitude. The Quechua, in contrast, are believed to be descended from different groups that were united under the Inca empire. Although they came to predominate numerically, territorially, and socially over the Aymara, the Quechua may have been biologically a more heterogeneous group.

Cruz-Coke et al. (1966) and Garruto and Hoff (1976) estimated Crow's (1958) Index of Opportunity for Selection (I) and its components, I_m (mortality) and I_f (fertility) in Quechua and Aymara populations. The value of the selection index was 0.827 for the Quechua and 1.581 for the Aymara. In both groups, the mortality component (I_m) was much larger than the fertility component (I_f). The values of I_m and I_f were, respectively, 0.522 and 0.200 for the Quechua population. For the Aymara population, the same components of the index were 1.178

and 0.185, respectively. These results establish that there has been potential for genetic change due to natural selection, particularly through differential mortality.

Natural selection cannot produce changes in the population mean of a quantitative trait unless additive genetic variation is present. From previous studies on the proportion of genetic variance in 20 anthropometric measurements collected from Camacani, Peru (Kramer 1980, Vandemark 1985, Ahn 1986; all this volume), it can be concluded that a substantial amount of environmental variance influences differences in body size and chest morphology of the Andean population; there are, however, measurable levels of genetic variance present as well. It also should be noted that those traits directly associated with the thoracic complex showed low heritability estimates. The relatively low heritability estimates for thoracic traits could reflect the possibility that directional selection for large chest volume might have caused the reduction in additive genetic variance as it shifted the population means for these traits.

In sum, there is substantial evidence to indicate that under extreme environmental stresses such as heat, cold, and high altitude, human populations survive, reproduce, and exhibit characteristic features of morphology and physiology that may have been shaped by adaptive processes.

RATIONALE AND OBJECTIVES

The human population investigated in this study resides in an area collectively referred to as the altiplano. The altiplano comprises the central Andean highland surrounding Lakes Titicaca and Poopo, at about 3,900 m of altitude. The altiplano is characterized by multiple environmental stresses that shape the existence of the human populations resident there. The short geological history of the mountains, which are about five million years old, results in a rugged topology and immature soils. The altiplano exhibits a distinctive climatic pattern (Eidt 1968). Precipitation is seasonal, with rainfall beginning in September, reaching a peak intensity in January, and ending in April. Droughts up to one year are common in the altiplano. But droughts resulting from irregularities in monthly precipitation can be equally devastating if they occur during the beginning of the planting season, around September or October. Diurnal temperature variation has a very wide range in the altiplano because of the sparse vegetation and thin atmosphere associated with high altitude. The daily high temperature, of approximately 17 degrees Celsius, occurs in the afternoon; on clear nights the temperature may fall below freezing. This diurnal variation creates the possibility for frost during any time of the year. However, in the Andes, the most pervasive environmental stress on human populations is hypoxia. Hypoxia is produced by the normal low partial pressure of

oxygen in the atmosphere at high altitude. Cultural adjustments (such as reduced levels of activity) are usually not sufficient to overcome this environmental stress.

Against this background of environmental stress, morphological and physiological adaptations should be expected as part of the adaptive complex that makes it possible for human populations to survive in the Andes. As described earlier, previous studies on adaptation to high altitude have led to the suggestion that natural selection has influenced human populations resident at high altitude. However, the nature and extent of natural selection has not yet been evaluated. Because peopling of the Andean high plateau began presumably 10,000 years ago, or perhaps 20,000 years ago (Vellard 1976), there has been enough time for natural selection to act. This study aims at measuring the current strength of selection on 20 anthropometric traits describing overall body size and thoracic dimensions between two generations in an Andean population. The underlying hypothesis is that natural selection has operated with differential degrees of magnitude on some or all of the anthropometric traits that relate to high-altitude adaptation. Also, this study may provide yet another example of how natural selection influences human evolution.

The population studied here resides in Camacani, a small village located on the shore of Lake Titicaca at an altitude of about 3,900 m in the Department of Puno, Peru. The village is immediately adjacent to an agricultural experiment station that is operated under the auspices of the Universidad Nacional Técnica del Altiplano. There are approximately 2,100 inhabitants of the village, chiefly of Aymara descent. Residents of Camacani are primarily engaged in agriculture, as are most others in this region. Their dietary staples include potatoes and quinoa as well as dairy products and fish as sources of protein. Most older adults have had relatively little formal education, but educational levels have been increasing steadily in more recent generations.

A set of 20 anthropometric measurements (Appendix A) was taken on both children and adults in order to describe overall body size, thoracic morphology and nutritional status. Measurements were taken with anthropometric instruments, following procedures prescribed in the IBP (International Biological Programme) handbook (Weiner and Lourie 1969). Separate questionnaires were distributed to children and adults. For children, the questionnaire was about sex, age, place of birth, and place of residence. For adults, nine socioeconomic questions were added in order to assess the extent of environmental homogeneity; a list of offspring and other relatives was also requested. In addition, adults were administered a general health survey designed to assess the overall health condition of the respondent, with a special focus on cardiovascular fitness. The next section will include description of selection methods, the

selection model applied to this study population, sampling methods and statistical analyses. The following section will present the results obtained from this study: patterns of age change, heritability estimates of 20 anthropometric measurements, genetic and phenotypic correlation coefficients between the traits and estimation of selection coefficients on them. These results will be discussed and concluded in the final section.

METHODOLOGY OF THE AYMARA STUDY

SELECTION METHODS

There are several methods for estimating fitness and the influence of natural selection, depending on whether one wishes to consider changes in the mean of a trait, the variance, or both mean and variance. Three types of these methods will be discussed here: direct univariate, univariate mean fitness, and multivariate methods (Endler 1986).

Direct Univariate Methods

Direct univariate methods, first developed by animal breeders, provide one simple approach. In this context, two measures of selection (Falconer 1981) are

$$i = \frac{\bar{x}_a - \bar{x}_b}{v_b}$$

$$j = \frac{v_a - v_b}{v_b}$$

where
$\bar{x}_a$: the mean value of a trait after selection

$\bar{x}_b$: the mean value of a trait before selection

v_a : variance of a trait after selection

v_b : variance of a trait before selection .

The quantity i is the standardized directional selection differential and the quantity j is the standardized variance selection differential. These symbols stand for the proportional changes in the mean and variance, respectively. Henceforth, in this discussion stabilizing and disruptive selection will be referred to collectively as variance selection, since they produce changes in the variance of a phenotypic distribution.

Because directional selection reduces genetic variance (Falconer 1981), multiple regression is suggested as a means of estimating independently selection on the mean and

variance. If the variance in fitness or the mean fitness is known and the trait is normally distributed,

$$i^* = \frac{i}{\sqrt{P}}$$

$$j^* = \frac{j + i^2}{\sqrt{P}} .$$

P is the variance in relative fitness. The parameter i^2 is proportional to the amount that the variance is reduced by directional selection. The two selectional coefficients (i^* and j^*) are the standardized multiple regression coefficients of relative fitness on mean and variance.

The direct univariate methods have an advantage over other methods of selection measures in that they can be used with the heritability of the trait to yield the genetic response to directional selection. This parameter can be used, in turn, to estimate the rate of selection. If the selection differential, i, applies to the parents, h^2 is the heritability of the trait, and R is the deviation of the mean value of the offspring of the selected parents from the population mean, then the standardized response is

$$\frac{R}{\sigma} = ih^2 \qquad \text{(Falconer 1981).}$$

However, these univariate methods ignore the effects of genetic or phenotypic correlations on the selection response. Phenotypic or genetic correlations among traits may produce i and R values that are larger or smaller than the true value. We would expect i or R values to be larger when indirect selection positively influences the trait through any correlated characters and to be smaller in the presence of negative indirect selection acting on that trait through any correlated characters.

Univariate Mean Fitness Methods

Univariate mean fitness methods require estimation of fitness or assumptions about fitness W(x) for each value x. A single statistic estimates the combined effect on fitness of directional and variance selection. There are two commonly used models for the operation of selection: truncation selection and change of mean fitness due to selection on the trait.

The truncation model assumes that there is some optimum value m at which fitness, W(m), is maximized. Haldane (1954) first proposed this measure as

$$H = \ln\left[\frac{W(m)}{\overline{W}}\right].$$

Later Van Valen (1973) developed an improved expression, in which

$$I = \frac{W(m) - \overline{\overline{W}}}{W(m)},$$

where the quantity I stands for the percentage of deaths due to the existence of individuals below the optimum value, m.

However, selection would almost never operate on absolute thresholds in natural populations. O'Donald (1968), Cavalli-Sforza and Bodmer (1971), and Manly (1975, 1976, 1977) remove the assumption of truncation selection by estimating I with consideration for the relationship between phenotypic value x and its fitness, W(x).

Linear model (O'Donald 1970):

$W(x) = d + kx$;

Double exponential model (Manly 1976):

$W(x) = \exp[\exp(d + kx)]$;

Quadratic model (O'Donald 1968):

$W(x) = 1 - a - k(m - x)^2$;

Normal model (Cavalli-Sforza and Bodmer 1971):

$W(x) = (1 - a)\exp[-k(m - x)^2]$.

In all of the preceding models, the parameters d, k and a are constant in a particular population. The quantity a is 1-absolute fitness at the optimum (x=m). In the quadratic and normal models, fitness reaches a maximum at an intermediate trait value m, while in the linear and double exponential models fitness either increases or decreases with x. Thus, the quadratic and normal models are most appropriate for systems in which variance selection may occur, while the other two models are more suitable for situations where directional selection predominates. However, because there is no optimum value in either the linear or the double exponential model, neither can be used to estimate I. In addition, no distinction between effects of directional selection and variance selection can be derived from the estimate I in any of these cases.

On the other hand, if the frequency of a phenotypic distribution, f(x), and W(x) are known before and after selection, then $\overline{W}_b$ and $\overline{W}_a$ can be calculated directly from two successive samples. A measure of the relative change in $\overline{W}$ as a result of selection in a certain interval between the samples is

$$I_W = \frac{\Delta W}{\overline{W}_b}$$

$$= \overline{W}_a - \overline{W}_b$$

$$= \frac{V_b}{\overline{W}_b^2} \quad \text{(O'Donald 1970).}$$

This expression explains Fisher's (1930) fundamental theorem of natural selection, apart from the effect of heritability: natural selection acts directly on the portions of individuals' phenotypes which are genetically controlled. Therefore, changes in the frequencies of the phenotypes due to natural selection generally continue as long as there is genetic variation in a population and the rate of change is directly proportionate to the amount of variation.

Instead of measuring the observed rate of selection, we can estimate the maximum rate that is possible in a given population, given its genetic variation, population structure, and so forth (Crow 1958). If there are only two absolute fitness classes (W=0 or W=1), then

$$P = \left[\frac{1 - \overline{W}}{\overline{W}}\right]\left[\frac{n_b}{n_b - 1}\right]$$

where

n_b : sample size before selection

$\overline{W}$: the mean absolute fitness

P : opportunity for selection.

The parameter P can be used as an upper limit to the overall action of selection. However, the opportunity for selection is intended for predictions of future response to selection rather than a population's present experience or past history of selection.

Multivariate Methods

Selection does not, as a general rule, operate on single traits in isolation. Traits may be phenotypically and genetically correlated with each other, so that selection on one trait may indirectly influence phenotypic selection on a phenotypically correlated trait. The result would be a correlated response to selection to the extent that there is also a genetic correlation among the traits (Falconer 1981).

A more direct estimate of the contribution to fitness of many traits can be obtained by multiple regression. Cornfield (1962), Manly (1975, 1976, 1977), and Lande and Arnold (1983)

independently devised models and methods. In each, an estimate is made of the function relating the fitness of an individual (W) to each trait value x_k.

Lande-Arnold model:

$W = a + \Sigma b_k x_k$;

Cornfield model:

$W = 1 / [1 + \exp(a + \Sigma b_k x_k)]$;

Manly model:

$W = \exp[-f(t)\exp(a + \Sigma b_k x_k)]$.

In all of the preceding models parameter a is constant and b_k stands for regression coefficient.

In the Manly model, $f(t)$ is a positive, nondecreasing function of time t such that $f(0)=0$. This parameter, $f(t)$, was chosen because Manly's model was explicitly designed to deal with only the survival component of natural selection. That is, W is the probability of surviving to time t. The double exponential function was chosen for the same reason and also because Manly designed the method for repeated sampling of cohorts. Cornfield adapted the logistic form of expression because of the discontinuous nature of his classification of individuals into high and low fitness.

Following an approach pioneered by Pearson (1903), Lande and Arnold (1983) derived a multivariate statistical method for measuring selection solely from observed changes in the distribution of phenotypic characters in a population within a generation. Their model is general and does not require an explicit assumption about the relationship between W and x. Just as do Lande and Arnold, Cornfield estimates the constant a and the coefficient b_k by means of multiple regression, while Manly estimates them by a maximum-likelihood method.

The method developed by Lande and Arnold for measuring different types of selection will be applied to the anthropometric data from a high altitude Aymara population treated in this study. The next section will describe the selection model used by Lande and Arnold.

THE SELECTION MODEL APPLIED TO AN AYMARA POPULATION

Directional Selection

Consider the effect of selection on the genetic evolution of the mean phenotype in a population. The phenotypic value (z) before selection is the sum of the breeding value (x) and the non-additive genetic effects (e) in the absence of genotype-environment interaction or correlation, such that

$z = x + e$,   where $\bar{e} = 0$.

The phenotypic variance-covariance matrix (P) can be expressed as

$$P = G + E,$$

where P symbolizes the phenotypic variance-covariance matrix, G represents the additive genetic variance-covariance matrix, and E stands for the nonadditive genetic variance-covariance matrix.

If the regression of breeding values on phenotypic values is assumed to be linear and homoscedastic, then

$$x - \bar{x} = GP^{-1} (z - \bar{z}) + e, \quad \text{where } \bar{e} = 0.$$

Pearson's study (1903) demonstrates that phenotypic selection does not change the coefficients in the above regression. Therefore, the change in the mean breeding value produced by phenotypic selection within a generation is

$$\bar{x}^* - \bar{x} = GP^{-1} (\bar{z}^* - \bar{z}).$$

Without change in the mean environmental effect between generations or operation of forces of evolution other than selection, the mean breeding value of selected parents is equal to the mean phenotype of their offspring. The directional selection differential is defined as the change in the mean value of a phenotypic character produced by selection within a generation (Falconer 1981) such that

$$S = \bar{z}^* - \bar{z},$$

where S is the vector of the directional selection differential, $\bar{z}^*$ is the vector of mean value of a character after selection, and $\bar{z}$ is the vector of mean value of a character before selection.

The resultant change in the mean phenotype across one generation produced by selection is

$$\Delta\bar{z} = GP^{-1}S.$$

In order to measure the direct effect of directional selection, the observed directional differential is partitioned such that

$$s_i = \Sigma P_{ij}\beta_j,$$

where β_j is the partial regression coefficient of relative fitness on the jth character as the directional selection gradient. The vector of partial regression coefficients is given by the expression,

$$\beta = P^{-1}S.$$

The observed selection differential on a particular character can be expressed in terms of phenotypic standard deviations,

$$s'_i = s_i/\sigma_i.$$

Also, the directional selection gradient is standardized such that

$$\beta'_i = \beta_i \sigma_i.$$

This measure is the coefficient in the linear regression of relative fitness on the standardized characters.

Variance Selection

Assume a multivariate normal phenotype distribution for the characters in a population before selection. The observed change in the phenotypic variance-covariance matrix after selection within a generation is

$$P^* - P = Cov[w, (z - \bar{z})(z - \bar{z})^T] - SS^T,$$

where P^* is the phenotypic variance-covariance matrix after selection, P is the phenotypic variance-covariance matrix before selection, w is the relative fitness, and S is the vector of directional selection differential. The first term in this expression represents the covariance of relative fitness with a matrix of quadratic deviations of the characters from their mean values. This is the matrix of observed variance selection differential, symbolized by C. The second term is the change in P caused by directional selection. The variance selection differential is independent of directional selection.

The variance selection gradient, γ, measures the forces of variance selection acting directly on the characters, independent of the forces of directional selection, and can be expressed as

$$\gamma = P^{-1}CP^{-1}.$$

The diagonal elements measure the strength of variance selection directly on the variance of each character, and the off-diagonal elements indicate the strength of selection directly on covariances. This measure can be standardized such that

$$\gamma'_{ij} = \gamma_{ij}\sigma_i\sigma_j.$$

The measure γ'_{ij} is the coefficient in the quadratic regression of relative fitness on the standardized characters.

As a usual assumption of regression, the errors around the regression surface must be uniform over all values of the traits (homoscedastic), and the traits must be multivariate normal. In addition, quadratic multiple regression can be used to estimate the stabilizing or disruptive selection on each trait, after removing the effects of direct selection. Multivariate methods have the great advantage that they entirely avoid the problems that result from estimating selection on individual traits separately and then combining them in some arbitrary way. For example, the problem of "genetic load" is entirely avoided by this analysis. During the genetic load controversy (Wallace 1981), fitnesses with respect to different loci were

combined in a completely arbitrary way. This is no longer necessary because, given a particular distribution of alleles at many loci, multiple regression estimates show how a particular combination of trait values affects the probability of survival (or some other component of fitness). The combinations can be estimated explicitly.

A major problem in multivariate analysis is caused by missing variables. If an important major independent variable is not included in the study, then the apparent importance of the known variables will be inflated, and in some cases (depending upon correlations of other variables with the missing factor) the sign of the observed regression coefficient can even be changed. To avoid this potentially serious problem, some optimum number of functionally significant traits must be chosen for analysis.

For each trait, very large sample sizes are necessary in order to get reliable estimates of the regression coefficients, since only a few aberrant points can radically change the observed values. With smaller sample sizes (i.e. less than 100) the methods are extremely sensitive to the addition or subtraction of variables (Sokal and Rohlf 1981). The total sample size must be larger than the total number of traits for the model to be applicable at all, and it must be considerably larger to yield significant regression coefficients. In formal terms, the sample size in multiple regression should be at least the number of characters (t) plus $t(t + 1)/2$ (Lande and Arnold 1983).

Another important problem with multiple regression, especially quadratic regression, is that the estimation of the γ values is extremely sensitive to intercorrelation of the independent variables, which can lead to a singular P matrix, invalidating the estimates. This is a particular problem in data sets characterized by few variables and small sample sizes. In a set of t strongly intercorrelated traits, $t-1$ should be deleted from the analysis.

The following section will discuss two methods of data collection that commonly are used in empirical studies of selection.

Sampling Methods

There are two distinct ways to collect data for the study of selection: longitudinal and cross-sectional studies. In the longitudinal approach, individuals usually are observed through a span of time to score some components of fitness, as well as a set of phenotypic characters, for each individual. This is the most direct method for detecting natural selection because it tests specifically for fitness differences and also can yield data on inheritance. In addition, this is the only method by which it is possible to obtain complete lifetime fitness estimates, which are required in order to predict changes in or equilibria of phenotypic frequency distributions.

In the cross-sectional study, simultaneous samples are taken of all age classes at a specific time; these can be used to measure fitness differences. If the cross-sectional study includes data from parents and their offspring, then information is also obtainable for studies of inheritance.

A major difference can be seen between the longitudinal and cross-sectional approaches to collecting data. In the cross-sectional study, there are no data on the relative success of individuals, while there can be such data in the longitudinal study if individuals, rather than cohorts, are individually marked and studied through their lifespans. Cross-sectional analysis infers fitness differences for the purpose of studying natural selection by measuring differences in trait frequency distributions among age classes, while longitudinal analysis measures temporal changes in fitness differences directly.

The principal drawback of the comprehensive longitudinal study, however, is the time it takes to complete and the relatively small number of subjects that usually can be followed. For this reason, very few attempts at lifetime fitness measurement have been made (McGregor et al. 1981, Clutton-Brock et al. 1982). In contrast, cross-sectional analysis can be used when it is impractical to do longitudinal analysis. Some cross-sectional studies have been done on comparisons between juveniles and adults (Weldon 1901, Dowdeswell 1961, Berry et al. 1979), between living and dead individuals (Bumpus 1899, Richardson 1974), and also among two or more age classes (Berry and Crothers 1968, Hiorns and Harrison 1970).

The following section will demonstrate how cross-sectional data are used in order to test the selection model.

Statistical Analyses

The selection model developed by Lande and Arnold (1983) was applied to the high-altitude Peruvian population that is the focus of this study. The first reason for adopting this approach is that this data set has information on phenotypic values, rather than fitnesses, of anthropometric traits. In addition, this study contains data on parents and their offspring, so information is available on the inheritance of the traits under study. Another reason is that this data set is large enough to permit reliable estimation of genetic parameters. Finally, the main purpose of this study is to examine the direct effect of natural selection on a particular trait of this high-altitude population. The multivariate method employed here permits estimation of the direct effect of selection on a set of traits, apart from the indirect effects of selection on phenotypically correlated traits.

The following procedures have been carried out in the multivariate statistical method for measuring the strength of selection.

Step 1: A set of 20 anthropometric traits (defined in Appendix A) was measured on each of 807 subjects in this sample.

The anthropometric measurements were standardized by age and sex in order to make it possible to compare individuals of different ages and sexes. Each individual's raw values were converted into z-score deviations from the mean of the specific parameter for a particular age and sex class. This approach corrects for inequality of variances between sexes and also removes absolute differences between cohorts.

Step 2: Normality of the frequency distribution of traits was examined, since this selection model assumes a normal distribution of phenotypes. There are several ways to test for normality (Johnson and Wichern 1982). One way to check normality is by using the normal probability (Q-Q) plots of data. These plot the sample quantile (X_i) against the quantile (Q_i) that one would expect to observe if the observations actually were normally distributed. When the points lie very nearly along a straight line, the assumption of normality remains tenable. The Q-Q plots are not particularly informative unless the sample size is moderate to large; for instance, $n \geq 20$. Quite a bit of variability can exist in the straightness of the plot for small samples, even when the observations are known to come from a normal population.

A second approach is to examine the correlation coefficients between X_i and Q_i. The straightness of the Q-Q plot can be measured by calculating the correlation coefficient of the points in the plot. The correlation coefficient between X_i and Q_i (r_Q) is computed by Pearson's product-moment correlation coefficient. This provides a powerful test of normality. Formally, we can reject the hypothesis of normality at the level of significance α if r_Q falls below the critical value.

The last test involves the Kolmogorov D statistic, which tests the null hypothesis that the input data values are a random sample from a univariate normal distribution. This Kolmogorov D is used when $n > 50$; for smaller samples, the Shapiro-Wilk statistic (W) is computed.

Step 3: After the forms of the trait distributions were checked, natural log-transformation was used to adjust the distributions of these traits which did not show normality. Log-transformation can reduce the degree of skewness in the Q-Q plot. In addition it may remove or reduce variance attributable to epistatic interactions or genotype-environmental interactions. The frequency distribution of any quantitative trait usually

approximates more or less closely to a normal curve, particularly if the sample size is large enough.

Step 4: Full sib data are used to estimate the matrix of additive genetic variance and covariance. If partial dominance does not lead to serious overestimation of trait correlation as mentioned by Arnold (1981), full sib families can be used. Estimates of heritability in the full-sib analysis should be viewed as establishing upper limits for the magnitude of the parameter h^2. These expected results were supported by our previous studies (Kramer 1980, Vandemark 1985, Ahn 1986; all this volume). Common family environment also can inflate the estimate of h^2 and genetic correlation (Falconer 1981). However, the experimental studies (Burghardt 1971, Arnold 1981) showed no confounding of a common family environmental effect with a genetic effect.

Multivariate analysis of variance (MANOVA) is applied to estimate the matrix of additive genetic variance-covariance (Johnson and Wichern 1982). In the MANOVA model,

$$Y_{ik} = \mu + \alpha_i + e_{ik} \text{ where } k = 1,2,\ldots, n_i \text{ and } i = 1,2,\ldots, g$$

and where Y_{ik} is a vector of observations on the kth individual from the ith family, and e_{ik} are independent $N_p(0, \Sigma)$ variables. Here, the covariance matrix Σ is constant. The parameter vector μ is an overall mean and α_i represents the ith family effect with $\Sigma_{i=1}^{g} n_i \alpha_i = 0$.

Table 1. Multivariate Analysis of Variance

Source of variation	d.f.	SSP	MS	EMS
Between families	g-1	B	B/(g-1)	$\sigma^2_w + k\sigma^2_s$
Within families	N-g	W	W/(N-g)	σ^2_w

In the notation used here and in Table 1, d.f. stands for the degrees of freedom, SSP is the matrix of sums of squares and crossproducts, MS is the matrix of mean squares and crossproducts, EMS is the matrix of expected MS, N is the total number of individuals, g is the number of families, n_i is the number of individuals within the ith family, k is n_i in expected mean squares, σ^2_w is the component of variance attributable to individuals within full-sib families, and σ^2_s is the component of variance attributable to families.

The MANOVA analysis shown in Table 1 is exactly the same form, component by component, as the ANOVA (Analysis of Variance) table, except that squares of scalars are

replaced by their vector counterparts. Consequently, covariance between two characters can be obtained from the product of the value of X in one member of a family and the value of Y in the other of the same family. A Pascal program has been designed for estimation of components of variances and covariances.

The genetic correlation matrix also can be estimated from the additive genetic variance and covariance matrix. Genetic correlation is the standardized genetic covariance which reflects the degree of pleiotropy and linkage of genes underlying variation for two phenotypic characters. However, the matrix of genetic correlation coefficients for 20 anthropometric traits (listed in Table 2 and defined in Appendix A) shows some values of genetic correlation coefficients that are larger than 1. They are highly correlated with each other by definition. So if the correlation coefficient is larger than 1, then it is better to choose one out of the two traits which show high correlation with each other.

Step 5: To estimate the matrices of phenotypic variance- covariance before and after selection, it is necessary to determine the age of each individual within each sex category at age of the first child because of overlapping generations in this sample. Next, individuals are categorized into two groups, the offspring group and the parental group. The offspring group consists of individuals below the youngest parent's age at the time of birth of the first child and the parental group contains those at or above the age at the time of the first child's birth.

The estimation of the phenotypic correlation coefficient matrix is used to identify the phenotypic relationships among the anthropometric traits.

Step 6: The change of mean values of anthropometric measurements is computed between the parental and the offspring group.

Step 7: The vector of the directional selection differential (S) and the vector of the directional selection gradient (β) are estimated using APL, a program language suitable for matrix and vector operations. The force of variance selection is also measured using APL. The formulas used in this step are as follows:

$$\Delta \bar{z} = GP^{-1}S$$
$$\beta = P^{-1}S$$
$$C = P^* - P + SS^T$$
$$\gamma = P^{-1}CP^{-1} .$$

In these formulas, $\Delta \bar{z}$ is the vector of the change in the phenotypic mean between the parental and the offspring group, G is the matrix of additive genetic variance-covariance for traits, S is the vector of directional selection differential, β is the vector of directional selection gradient, P^* is the matrix of phenotypic variance-covariance after selection, P is the matrix of

phenotypic variance-covariance before selection, C is the matrix of variance selection differential, and γ is the matrix of variance selection gradient.

High correlations between traits may cancel or reduce the true effect of selection on a particular trait. For example, in the analysis of data on pentatomid bugs, Lande and Arnold (1983) found that the thorax showed no significant selection differential. Nevertheless, the coefficient of selection gradient for the thorax is highly significant. These findings indicate that substantial selection directly on the thorax was masked in the selection differential by indirect selection through some correlated character(s). Furthermore, a high correlation may cause the matrix of variance-covariance in multiple regression to be singular, which invalidates the estimation of regression coefficients.

RESULTS

The cross-sectional sample consisting of 442 males and 365 females has been categorized into 32 age classes for each sex, as shown in Appendix B describing the age distribution of the Camacani Aymara population. This section summarizes the findings on the patterns of age change in 20 anthropometric traits represented by the cross-sectional samples. From these data, some inferences can be made about the influence of genetic and environmental factors on growth as well as secular changes.

Patterns of Age Change

Appendix C presents the cross-sectional patterns of change with age in the 20 anthropometric traits included in this study. Growth in weight appears to continue until age 22 for males and age 17 for females. Sexual dimorphism in weight is not well defined until about age 16.

Males in this population show a gradual increase in stature up to age 22; in the case of females a comparable plateau is reached at about age 18. Sexual dimorphism in stature appears to begin at about age 15. Acromial height does not exhibit sexual dimorphism; however, its growth continues up to the age of 21 for males and 18 for females. Sternal length shows continuous growth until age 18 for males and age 14 for females; sexual dimorphism in sternal length is not well defined until about the age of 14.

When the patterns of growth in stature (HT), sitting height (SH), sternal length (STL) and acromial height (AH) are compared, they indicate that stature shows a more similar pattern to sitting height than acromial height; this may largely reflect the fact that the

former two measurements both incorporate neck and head heights while acromial height is a more straightforward measurement of trunk length. However, the three anthropometric characters all show much more similarity in the pattern of age change than does sternal length. These results agree with those obtained from the genetic distance matrix which will be described later on in this section, as well as with results reported previously by Eckhardt (1985). It might be inferred, therefore, that patterns of phenotypic distributions of anthropometric characters can help identify characteristic features of high altitude populations. These patterns may reflect underlying genetic influences on development from the population's gene pool.

Measurements of all skinfold thicknesses exhibit a generally similar pattern of age change. Skinfolds at the mid-axillary, triceps, suprailiac and subscapular points decrease sharply in the categories between age 1 and age 3 but increase rapidly afterward until, on average, age 9 for both sexes. Sexual dimorphism in skinfolds appears to occur as early as age 10. Females in general exhibit larger skinfold measurements than males at all ages. Measurements of triceps skinfolds for males remain relatively static, however.

Upper arm circumference stops increasing at about the age of 21 for males and age of 17 for females. Sexual dimorphism in this measurement is not well defined until about age 20. During adolescence, females are fatter than males.

Thoracic circumference continues to increase until about age 22 for males and age 20 for females. Sexual dimorphism in thoracic circumference is not well defined until about age 25, which is later than is observed for other traits. Substernal circumference stops increasing at about age 28 for males and age 19 for females. It also shows late sexual dimorphism, at around age 24. Patterns of age change in chest circumference indicate that despite their smaller statures, members of this high-altitude population develop greater chest circumferences than do comparable low altitude populations. In other words, they show an accelerated growth in thoracic size relative to stature.

The Nuñoa study carried out by Frisancho and Baker (1970) shows the same overall result as this study of an Aymara population. Growth in stature and body weight of the Quechua population appears to continue until age 22. On the other hand, growth in chest width and depth stops at age 19. Sexual dimorphism in body size is not well defined until about age 16.

The ratios of chest circumference to stature at high altitude, such as in Nuñoa males residing at around 4,000 m and above 4,500 m, are different from patterns seen in lowlanders. In the higher altitude group, especially between ages 14 and 18, chest circumference is

significantly larger than among populations residing at lower altitude. However, Eckhardt and Dutt (1979) have observed that the average Aymara male in the village of Camacani weighs 5 kilograms more than his Quechua counterpart in Nuñoa. Such observation is mainly due to the apparent better nutrition of the Camacani diet relative to the Nuñoa diet. Dietary staples in Camacani include potatoes and quinoa, as in Nuñoa, but the proximity of Camacani to Lake Titicaca makes the access to animal food sources easier than in Nuñoa. It is probable that Camacani residents consume more animal products per capita than Nuñoa residents, including more fat as well as more protein.

Linear chest dimensions exhibit patterns similar to those seen for circumferences. Anterior-posterior (A-P) diameter of the thorax stops increasing at about age 22 for males and age 19 for females. Sexual dimorphism in A-P diameter of the thorax is not well defined until about age 19. The A-P diameter at the level of the manubrium continues to increase up to age 22 for males and age 17 for females. Also, the sexual dimorphism in this trait appears to become manifest at about age 19. However, A-P diameter at the substernal level shows a continuous growth until about age 23 for males and age 20 for females. Sexual dimorphism is not well defined until about age 24. Anterior-posterior diameter at the substernal level shows a late sexual dimorphism.

Transverse diameter, which describes the width of the chest, shows a continuous growth until about age 18 for males and age 19 for females. Sexual dimorphism in this trait appears to occur at about age 19.

Biacromial diameter stops increasing at about age 22 for males and age 14 for females. Sexual dimorphism in this dimension is not well defined until about age 14.

Bi-iliac diameter continues to enlarge until about age 22 for males and age 24 for females. There is no evident sexual dimorphism in bi-iliac diameter. In summary, overall body size generally increases until about age 22 for males and age 17 for females. Sexual dimorphism in overall body size is not generally well defined until approximately age 16. On the other hand, thoracic measurements generally cease continuous growth at about age 22 for males and at about age 19 for females. The traits reflecting chest volume exhibit a late sexual dimorphism. This observation of a continual increase in dimensions is particularly evident in several of the non-standard measurements (sternal length, A-P diameter at the substernal level and substernal chest circumference) that were included in this study because of the *a priori* belief that they might better describe thoracic development than some of the standard IBP measurements. Overall, several of the non-IBP anthropometric measurements of thoracic size generally stop increasing at an earlier age than those of thoracic circumference.

The next section of this part summarizes the results from estimation of the heritability of anthropometric dimensions in this high-altitude Andean population. Heritability is regarded as an important statistic for the study of quantitative genetics in a population, and provides a simplified basis for understanding the results of the selection study provided later.

Heritability

Heritability can be defined in two ways. Heritability in the broad sense is the ratio of the genotypic variance to the phenotypic variance. Compared with heritability in the broad sense, heritability in the narrow sense (as studied here) can describe how much of the total phenotypic variation can be attributed to additive genetic effects. For twenty anthropometric traits, heritabilities already have been estimated in this high-altitude Peruvian population (Kramer 1980, Vandemark 1985, Ahn 1986; all this volume). In Table 2 heritability estimates obtained from regression analyses of offspring values on midparent values are arranged in order of decreasing magnitude, along with their respective standard errors.

The highest heritability estimate obtained was for stature, which was 0.509. For the chest measurements the results can be divided into two categories. One category shows moderate to low heritability estimates, ranging from 0.343 to 0.264. Included here are sternal length, A-P diameter at the substernal level, A-P diameter of thorax, and thoracic circumference at forced expiration. The next category exhibits low heritability estimates, ranging from 0.157 to 0. It includes thoracic circumference, transverse diameter of the chest, thoracic circumference at forced inspiration, A-P diameter at the level of the manubrium and substernal chest circumference. Among the subset comprising thoracic measurements only, traits which describe chest length and depth, such as sternal length, A-P diameter of the chest, and A-P diameter at the substernal level, have slightly higher heritability estimates. The A-P diameter at the level of the manubrium, which measures chest depth at the level of the clavicle, however, shows a quite low heritability estimate of 0.091. Overall, traits related to chest width and circumference have low heritability estimates. The traits with low to moderate heritability estimates seem to be precisely those which most accurately describe the characteristic features of the Andean thorax.

The heritability estimates for body weight and upper arm circumference are very close. They may share similarities in the effects of nutritional changes on the values of these measurements since these traits include the measurement of bone, muscle, subcutaneous fat and skin. It is interesting to point out that, when compared with heritability estimates for body

Table 2. Heritability Estimates

Trait	$\hat{h}^2$	s.e.
Stature	0.509	0.135
Upper Arm Circumference	0.413	0.067
Weight	0.400	0.066
Bi-iliac Diameter	0.388	0.062
Sternal Length	0.343	0.123
Subscapular Skinfolds	0.337	0.071
Sitting Height	0.337	0.070
Triceps Skinfolds	0.325	0.072
Suprailiac Skinfolds	0.321	0.079
Mid-axillary Skinfolds	0.299	0.064
A-P Diameter Substernal	0.286	0.117
A-P Diameter Thorax	0.280	0.103
Thoracic Circumference (Forced Expiration)	0.264	0.102
Thoracic Circumference (Normal)	0.157	0.103
Biacromial Diameter	0.149	0.069
Transverse Diameter Thorax	0.145	0.103
Thoracic Circumference (Forced Inspiration)	0.123	0.123
Acromial Height	0.118	0.059
A-P Diameter Manubrium	0.091	0.092
Substernal Circumference (Normal)	0.000	0.107

weight in sea level populations, the value is lower in this high-altitude Andean population. Although Roberts (1953) demonstrated that increases in body weight are proportional to decreases in temperature, reduced body weight is common in high-altitude Andean populations despite the cold environment. This may reflect the influence of marginal nutrition, a different gene pool, or even the effects of an interaction among hypoxia, cold and nutrition.

The heritability estimates for the four skinfold measurements are all very similar to one another, yet are notably smaller than those for body weight and upper arm circumference, traits which reflect elements of skin and fat. The lower heritability estimates for measurements on skinfold thicknesses may indicate that these measurements are the most susceptible to changes in dietary patterns or levels of physical activity (Vandemark 1985, this volume). This possibility could be investigated through serially repeated measurements on the same subjects over several years that included variation in nutrition and physical activity levels.

Bi-iliac diameter and sitting height had moderate heritability estimates, while acromial height and biacromial diameter had somewhat lower heritability estimates.

These results can be interpreted in different, though not necessarily contradictory ways. First, by definition the low heritability estimates for the chest traits imply the possibility of more substantial environmental influence on variation in the chest traits than on variation in traits describing body size. Nonadditive genetic effects or environmental influences may have contributed to the differential estimates between traits describing the thorax and those describing body size.

From a complementary perspective, however, the low heritability estimates obtained for the thoracic traits could reflect the operation of differential selection for chest and body size over past generations. As is known from other studies (Baker 1969, Clegg et al. 1970, Frisancho and Baker 1970, Frisancho 1976 and 1978, Beall et al. 1977, Beall 1982), Andean Indians at high altitude exhibit a large thorax relative to stature. Such allometric differences in proportion could result from selection operating more strongly on chest dimensions than on stature. This second explanation also could account for the relatively low heritability estimates for the measurements describing thoracic dimensions; since directional selection for large chest volume would reduce additive genetic variation as it shifted the population means for these traits.

The following section will describe the genetic and phenotypic correlation matrices for twenty anthropometric traits in order to characterize genetic and phenotypic relationships between traits.

Genetic and Phenotypic Correlation Matrices

A multivariate analysis of variance, using the Aymara family data mentioned earlier, estimated the genetic and phenotypic correlation matrices. As seen in Table 3, the genetic correlation coefficients vary in magnitude.

Table 3: Genetic Correlation Matrix

	WT	HT	STL	APT	TD	TCN
HT	0.712	HT				
STL	0.212	0.368	STL			
APT	0.635	0.363	-0.008	APT		
TD	0.713	0.241	-0.121	0.180	TD	
TCN	0.837	0.212	-0.217	0.429	1.042	TCN
UAC	0.777	0.359	-0.220	0.309	0.884	1.027
SS	0.556	-0.036	-0.151	0.180	0.658	0.788
SIS	0.485	-0.104	-0.278	0.285	0.529	0.938
MAS	0.334	0.005	-0.503	-0.042	0.811	0.827
TS	0.573	0.135	-0.220	0.129	0.758	0.924
AH	0.411	0.660	0.193	0.171	0.137	-0.199
BD	0.738	0.634	0.237	0.327	0.587	0.783
BID	0.712	0.510	-0.043	0.465	0.864	0.690
APM	0.277	0.075	-0.330	0.719	-0.170	-0.132
APS	0.754	0.275	0.252	1.022	0.292	0.680
TCFI	0.794	0.346	-0.062	0.475	0.902	0.958
TCFE	0.733	0.244	-0.164	0.437	0.848	1.134
SCN	0.757	0.178	-0.158	0.607	0.703	1.274
SH	0.612	0.790	0.293	0.233	0.158	0.046

	UAC	SS	SIS	MAS	TS	AH
SS	0.820	SS				
SIS	0.628	0.839	SIS			
MAS	1.110	0.785	1.163	MAS		
TS	0.987	0.708	0.880	1.257	TS	
AH	0.084	-0.150	-0.062	0.171	0.143	AH
BD	0.394	0.332	0.019	0.042	0.009	0.210
BID	0.742	0.373	0.582	0.062	0.714	0.091
APM	0.219	0.033	0.307	-0.006	0.321	0.125
APS	0.339	0.293	0.230	0.046	0.194	-0.058
TCFI	0.820	0.497	0.551	0.405	0.603	0.041
TCFE	0.857	0.659	0.642	0.657	0.709	-0.001
SCN	0.644	0.724	0.649	0.506	0.511	-0.287
SH	0.299	0.086	0.005	-0.035	0.186	0.912

	BD	BID	APM	APS	TCFI	TCFE
BID	0.402	BID				
APM	-0.224	0.185	APM			
APS	0.383	0.520	0.523	APS		
TCFI	0.607	0.695	-0.009	0.551	TCFI	
TCFE	0.569	0.664	-0.005	0.601	0.937	TCFE
SCN	0.722	0.617	-0.035	0.593	0.954	0.926
SH	0.491	0.349	-0.071	0.052	0.185	0.072

	SCN
SH	0.058

Table 4: Phenotypic Correlation Matrix

	WT	HT	STL	APT	TD	TCN
HT	0.664	HT				
STL	0.274	0.309	STL			
APT	0.548	0.341	0.336	APT		
TD	0.584	0.373	0.073	0.364	TD	
TCN	0.689	0.397	0.130	0.548	0.584	TCN
UAC	0.618	0.331	-0.007	0.361	0.560	0.559
SS	0.501	0.128	0.027	0.246	0.316	0.465
SIS	0.301	0.024	-0.110	0.165	0.376	0.295
MAS	0.348	0.101	-0.005	0.263	0.383	0.361
TS	0.267	0.009	-0.153	0.141	0.275	0.289
AH	0.334	0.498	0.207	0.208	0.233	0.209
BD	0.542	0.512	0.264	0.239	0.315	0.389
BID	0.545	0.445	0.014	0.241	0.401	0.448
APM	0.363	0.249	0.279	0.543	0.122	0.281
APS	0.56	0.299	0.218	0.791	0.393	0.582
TCFI	0.736	0.451	0.173	0.539	0.667	0.799
TCFE	0.734	0.400	0.149	0.554	0.639	0.825
SCN	0.583	0.318	-0.022	0.427	0.495	0.690
SH	0.535	0.686	0.280	0.273	0.300	0.327

	UAC	SS	SIS	MAS	TS	AH
SS	0.536	SS				
SIS	0.441	0.528	SIS			
MAS	0.495	0.548	0.505	MAS		
TS	0.504	0.546	0.554	0.600	TS	
AH	0.171	-0.033	0.012	0.117	0.027	AH
BD	0.331	0.314	0.042	0.129	0.015	0.166
BID	0.491	0.373	0.273	0.260	0.230	0.206
APM	0.198	0.082	0.030	0.143	0.029	0.141
APS	0.360	0.304	0.194	0.233	0.223	0.138
TCFI	0.595	0.441	0.340	0.358	0.253	0.233
TCFE	0.638	0.486	0.370	0.403	0.293	0.215
SCN	0.459	0.445	0.294	0.248	0.199	0.144
SH	0.249	0.100	0.001	0.096	0.044	0.692

	BD	BID	APM	APS	TCFI	TCFE
BID	0.355	BID				
APM	0.105	0.114	APM			
APS	0.216	0.288	0.377	APS		
TCFI	0.429	0.481	0.289	0.569	TCFI	
TCFE	0.401	0.447	0.326	0.594	0.851	TCFE
SCN	0.349	0.459	0.132	0.529	0.678	0.724
SH	0.361	0.245	0.176	0.239	0.345	0.321

	SCN
SH	0.258

Some genetic correlation coefficients indicate no genetic relationships between two traits such as sternal length (STL) and A-P diameter of the thorax (APT), sternal length and bi-iliac diameter (BID), A-P diameter of the thorax and skinfolds at the mid-axillary point (MAS), thoracic circumference (TCN) and sitting height (SH), and so on. Phenotypic correlation coefficients in Table 4 are generally positive, ranging from 0 to 0.825 in magnitude.

As compared with phenotypic correlation coefficients, genetic correlation coefficients tend to be higher and there are many negative correlation coefficients, although most are positive.

Differing from their phenotypic counterparts, some genetic correlation coefficients exceed the theoretical upper limit of + 1.0, undoubtedly a consequence of the particularly low estimates of heritability for these traits (Leamy 1974). Hill and Thompson (1978) determined the probability of obtaining negative semidefinite genetic covariance or genetic correlation matrices (matrices with ordinary or partial correlations greater than one or less than negative one and thus containing linear combinations with negative heritability), given certain sample sizes, numbers of traits, and levels of heritability. They found that the probability can approach 100 per cent even for fairly large samples. In general, the probability of obtaining such estimates, corresponding to theoretically impossible sets of genetic correlations, increases dramatically as the number of traits included in the analysis increases, but decreases with increasing sample size and heritability of the characters.

The results showed that there are sets of anthropometric traits that are highly correlated genetically.

These sets are:

(APT, APS)

(TD, TCN)

(TCN, UAC, SIS, MAS)

(TCN, TCFI, TCFE, SCN)

(UAC, MAS, TS)

(SIS, MAS, TS)

(AH, SH).

Appendix A gives definitions of these traits.

Given the high genetic correlations between traits, some of them can be excluded from further analyses without losing any genetic information. Therefore, eight traits concerning body size and chest size were chosen from the twenty anthropometric measurements in order to estimate the strength of selection. They are HT (Stature), STL (Sternal Length), APT
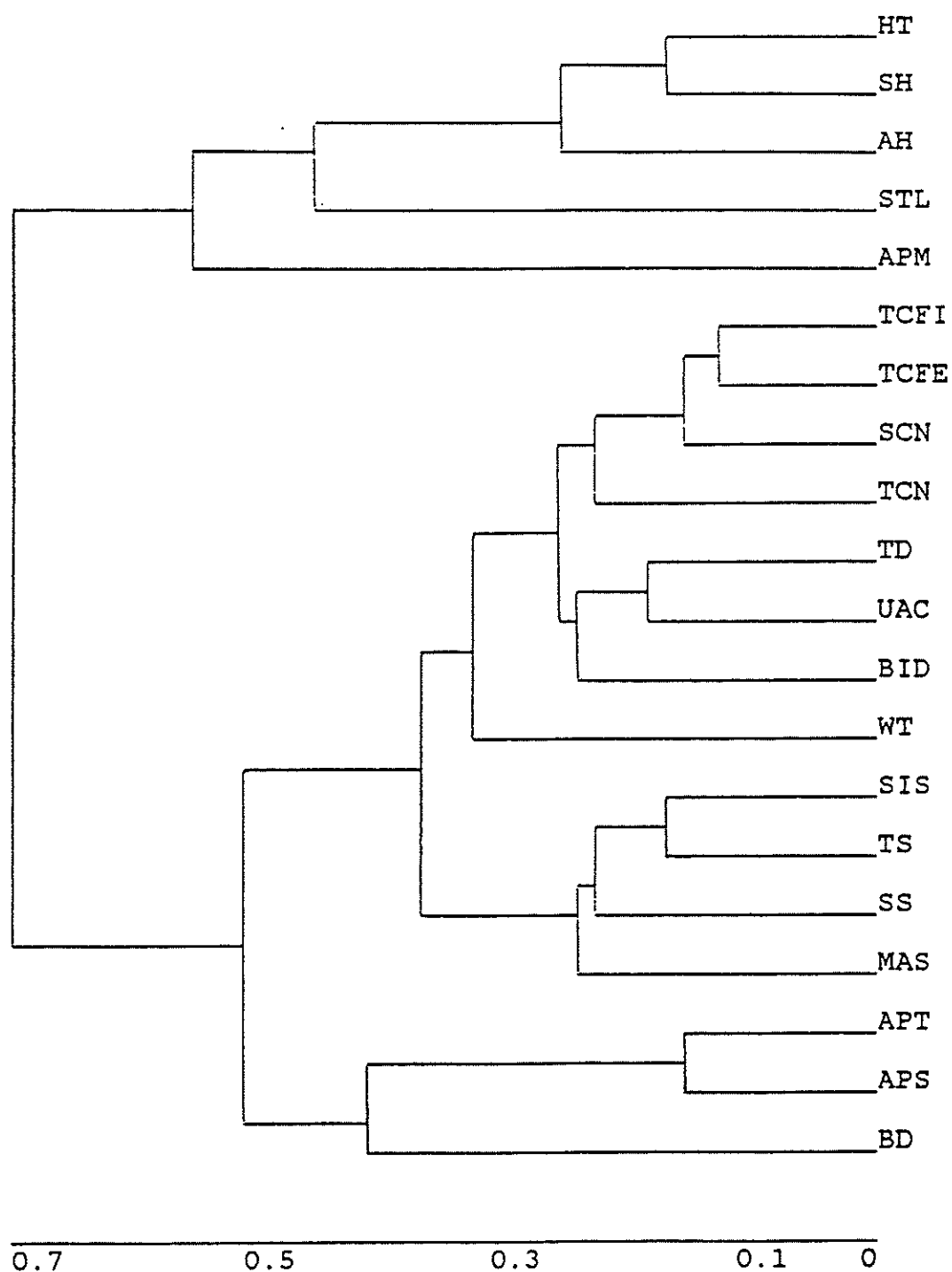
Figure 1: Distance Map Obtained from Genetic Correlation Matrix
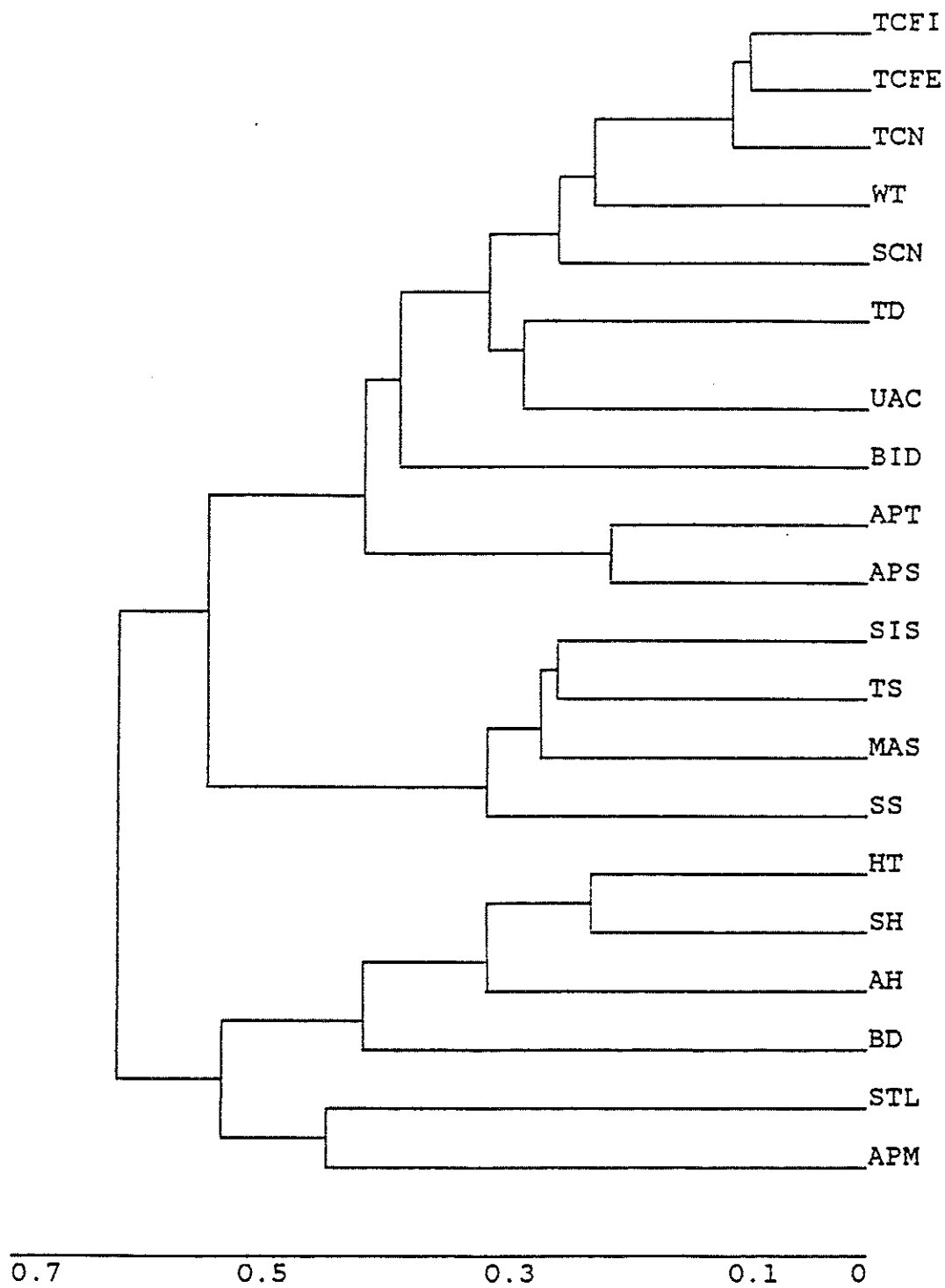
Figure 2: Distance Map Obtained from Phenotypic Correlation Matrix

(Anterior-Posterior Diameter Thorax), TD (Transverse Diameter), AH (Acromial Height), BD (Biacromial Diameter), BID (Bi-iliac Diameter), and APM (Anterior-Posterior Diameter Manubrium).

In order to examine the similarity of patterns between the genetic and phenotypic correlation matrices, average linkage clustering patterns within the genetic correlation matrix can be represented by a dendrogram. This clustering technique starts with the individual objects. Thus there are initially as many clusters as objects. Most similar objects are first grouped, according to their similarities. Eventually, as the similarity decreases, all groups are fused into a single cluster. For average linkage, groups are fused according to the average distance between pairs of members in the respective sets.

The genetic distance map in Fig. 1 shows four major clusters. Cluster 1 represents longitudinal measurements, which include stature (HT), sitting height (SH), acromial height (AH), sternal length (STL) and A-P diameter at the level of the manubrium (APM). Cluster 2 can be divided into 3 subclusters: anthropometric measurements on thoracic circumference; traits indicating fat and muscle on the thorax, upper arm, and pelvis; and body weight. Cluster 3 consists of measurements on skinfolds. This cluster is more closely related with cluster 2 than the others. The last cluster includes anthropometric traits describing the depth of chest and the breadth of shoulders. In this cluster, A-P diameter of the chest (APT) and A-P diameter at the subscapular level (APS) are closely related genetically with each other. This distance map obtained from the genetic correlation matrix tells that traits in each cluster share many genes with pleiotropic effects compared with the rest of traits in other clusters. Since quantitative characters generally are polygenic and many mutations are pleiotropic, different loci often must influence overlapping sets of characters. Groups of loci with overlapping pleiotropic effects often result from original identical duplicate genes that have evolved some specificity of expression in certain tissues, developmental stages and/or biochemical reactions (Lande 1980b). For example, stature and sitting height show a closer genetic relationship, as well as similar pattern of age change, as mentioned previously in this section. Measurements on thoracic depth and width are, however, relatively distant genetically from other anthropometric measurements.

A dendrogram was derived from average linkage clustering of the phenotypic correlation matrix in Figure 2. It exhibits two major clusters: longitudinal vs. non-longitudinal anthropometric traits. Cluster 1 is divisible into three subclusters: a subcluster including measurements on chest circumference, those on fat and muscle of the arm, pelvis and overall body; a subcluster of traits indicating the depth of the chest; and a last subcluster consisting of

measurements on skinfolds. On the other hand, cluster 2 has two subgroups: one group of traits indicating longitudinal body size and the breadth of shoulders; the other group including traits related to chest dimensions.

In general, the cluster analysis of genetic correlation coefficients produces a similar clustering pattern to that of phenotypic correlation coefficients, even though the latter may reflect differential nonadditive genetic factors. For example, the traits related to the depth of the chest, such as APT and APS, are less influenced by nonadditive genetic sources of variation while the traits of skinfolds thickness are strongly influenced by nonadditive genetic factors. Thus it could be said that the phenotypic correlation matrix (or variance-covariance matrix) is not significantly different from its genetic counterpart in this population.

Cheverud (1988) investigated the magnitudes and patterns of relationship within genetic and phenotypic correlation matrices. He demonstrated that when the sample size is large enough, genetic correlation estimates were only slightly greater than the corresponding phenotypic correlation estimates, and the patterns of correlations were strikingly similar. However, if genetic correlations were on average much higher than phenotypic correlations and genetic and phenotypic correlations had only broadly similar patterns, differences between genetic and phenotypic correlation estimates could arise due to disjunction between patterns of environmental and genetic effects on the developing phenotype and/or due to random sampling error present in estimates of true population values.

It seems likely, therefore, that in this study actual population values for genetic and phenotypic correlations are quite similar. The broad similarity of genetic and phenotypic correlation matrices indicates that genetic and environmental effects on development typically produce similar patterns of phenotypic variation. Phenotypic variation, which initially results from the combined action of the environment and the genotype, is dominated by the genotype under the same environmental influence and can be altered by selection.

Multivariate Measures of Selection

Table 5 presents estimates of directional selection and variance selection for eight anthropometric traits, instead of the twenty traits described in the previous sections.

The reason for dealing with the result of only eight traits in the study of selection is that, as noted earlier, some traits are highly correlated with respect to phenotype. Such high correlation can cause violation of the assumption underlying this selection model, that a phenotypic variance-covariance matrix is nonsingular. Thus only eight traits concerning body size and thoracic dimensions have been chosen. The eight anthropometric traits included here

Table 5. Estimates of Selection

TRAIT	S	S'	β (s.e.)	β (s.e.)	γ	γ'
HT	-0.029	-0.030	-0.162 (0.065)	-0.160 (0.063)	-3.340	-3.119
STL	0.045	0.047	0.409 (0.059)	0.393 (0.057)	-1.560	-1.434
APT	-0.019	-0.019	0.600 (0.072)	0.574 (0.069)	4.490	4.118
TD	0.245	0.264	0.214 (0.062)	0.199 (0.057)	-4.420	-3.801
AH	-0.318	-0.336	0.532 (0.061)	-0.504 (0.058)	-4.662	-4.182
BD	0.191	0.201	0.334 (0.060)	0.318 (0.057)	-6.462	-5.867
BID	-0.350	-0.376	-0.458 (0.060)	-0.426 (0.056)	-2.041	-1.766
APM	0.522	0.553	0.928 (0.067)	0.876 (0.063)	0.576	0.513

were chosen chiefly because of their descriptive value for this population, as inferred from previous studies. Also, of all anthropometric traits reflecting overall body size, only linear dimensions are dealt with in this study. They are stature, sternal length, A-P diameter of the thorax, transverse diameter of the chest, acromial height, biacromial diameter, bi-iliac diameter and A-P diameter at the level of the manubrium.

Coefficients of directional selection differential were calculated as the covariances between relative fitness and each character, as described in the section on methodology. They represent the changes in character means produced by direct and indirect selection. Directional selection gradients were estimated from the partial regression coefficients of relative fitness on the characters.

Stature (HT) shows the standardized directional selection gradient (β') of -0.16 and the standardized directional selection differential (S') of -0.03. The results indicate that weak selection takes place directly for reduction in stature. However with a smaller and opposite influence of indirect selection through correlated characters, this trait appears to show no appreciable change in its mean value.

For transverse diameter of the chest (TD), the standardized directional gradient of 0.199 shows that this trait is under weaker, positive directional selection and the standardized directional differential of 0.264 also shows some indirect influence of selection acting on correlated traits in the same direction. These findings suggest that selection acts weakly to broaden the thorax.

The standardized directional selection gradient, $\beta' = 0.318$, for biacromial diameter (BD) indicates that moderate selection may directly influence increases in this trait. The standardized directional selection differential for this trait, $S'=0.201$, indicates a weak effect of indirect selection counteracting the increase in biacromial diameter by direct selection.

For sternal length (STL), the standardized directional selection gradient of 0.393 implies a moderate effect of direct selection on this trait. It implies that sternal length tends to be increased by direct selection. However the direct effect of selection on sternal length is masked by a large influence of other indirect effect of selection acting on correlated traits. Consequently, sternal length appears to show no substantial net change in its mean value.

For bi-iliac diameter (BID), the estimate of the standardized directional selection gradient is -0.426 and the coefficient of the standardized selection differential is -0.376. Bi-iliac diameter thus tends to be decreased by direct effect of selection with little additional influence from indirect selection.

The standardized directional selection gradient for acromial height (AH) is -0.504, indicating that substantial selection acts directly to decrease acromial height. In addition, the standardized directional selection differential for acromial height, the coefficient of which is -0.336, tells that this trait tends to be decreased in size even under the slight negative force of indirect selection.

For A-P diameter of the thorax (APT), the standardized directional selection gradient is 0.574, indicating the existence of a significant effect of direct selection. Thus, selection strongly acts on this trait to increase the depth of the thorax. However, large effects of indirect selection through correlated characters occur in the opposite direction, obscuring the direct effect of selection on this trait.

As for A-P diameter of the thorax, A-P diameter at the level of the manubrium (APM) is directly under strong influence of selection. These measures of selection show that, regardless of the small influence of indirect selection in the opposite direction, A-P diameter at the level of the manubrium tends to be increased by direct effect of selection.

In Figure 3, the comparison of magnitude between the additive genetic variance and the directional selection gradient indicates that, if additive genetic variance is small, the directional selection gradient is large. Otherwise, the directional selection gradient is small. This pattern implies that directional selection has acted more strongly on the traits now exhibiting lower level of additive genetic variance than on those with large additive genetic variances.

The variance selection gradients were estimated from a quadratic multiple regression of relative fitness on the eight characters. The coefficients of standardized variance selection gradient (γ) in Table 4 show that disruptive selection acts on variances, particularly for A-P diameter of the thorax and A-P diameter at the level of the manubrium, while stabilizing selection acts on the remaining six traits even with different magnitudes of forces.

From these results, it can be said that selection has not acted strongly on characters related to overall body size such as stature but rather on those concerning thoracic dimensions, especially chest depth and length. Therefore, a larger volume of the chest appears to be selected for at high altitude.

Figure 3. A Comparison of the Orders of Magnitude for Additive Genetic Variance and Gradients of Directional Selection

Additive genetic variance:

HT	>	TD	>	BD	>	BID	>	APT	>	STL	>	AH	>	APM
(0.255)		(0.18)		(0.176)		(0.169)		(0.151)		(0.148)		(0.141)		(0.106)

Directional selection gradient:

HT	<	TD	<	BD	<	STL	<	BID	<	AH	<	APT	<	APM
(-0.16)		(0.20)		(0.32)		(0.39)		(-0.43)		(-0.50)		(0.57)		(0.88)

DISCUSSION AND CONCLUSIONS

In high-altitude Andean Indians, large chest size relative to stature is one of the most striking features in comparison to populations long resident at sea level. Some studies have suggested that this combination of phenotypic distinctions is the result of developmental acclimatization that occurs in each generation in response to environmental stress (Frisancho and Baker 1970, Frisancho et al. 1975, Lahiri et al. 1976, Cruz-Coke 1978, Stinson et al. 1978, Leonard 1989). Other studies propose that the adaptive complex could have resulted from genetic influences shaped by natural selection (Hurtado 1932a and 1971, Garruto and Hoff 1976, Beall et al. 1977, Vandemark 1985 and this volume, Ahn 1986 and this volume, Ahn and Eckhardt 1988). As described in the introduction, it is known that microevolution has occurred by means of natural selection in many populations, including humans, when they have faced

new environmental challenges. Hypoxia (normal low pressure of oxygen in the atmosphere) is the most pervasive environmental stress in the Andes.

From the patterns of age change in twenty anthropometric measurements in a high-altitude Peruvian population, it can be inferred that the influences of genetic and environmental factors act together, as might be expected. Compared with data derived from the U.S. (Stoudt et al. 1960) and data on Peruvian samples from sea level (Preto and Calderon 1947), Andean children at high altitude are absolutely and relatively smaller. However, they develop systematically greater chest circumferences, averaging about eight to ten per cent above Americans and other lower-altitude counterparts. Thus the thoracic dimensions of children at high altitude show accelerated growth.

Compared with Quechua children living at high altitude in Nuñoa, Aymara children in Camacani, at a similar altitude, are substantially similar in overall body size and chest diameters. However, in the age between 19 and 25 years, the Aymara are heavier and taller than the Quechua. In contrast, chest diameters differ by less than 1 cm from those in the Nuñoa population (Eckhardt and Dutt 1979). The difference in overall body size between the two populations can be explained not only by the apparently greater nutritional adequacy of the Camacani diet relative to the Nuñoa diet but also by greater heterogeneity in the groups of Quechua ancestry. The finding that there are no significant differences in chest dimensions between the two ethnic groups implies that they might share some common genes related to larger thoracic dimensions, as well as some common developmental responses, resulting from adaptation to high altitude.

In a study of genetic continuity from high altitude to low altitude (Ahn and Eckhardt 1988), growth patterns of 20 anthropometric dimensions were compared between two Peruvian groups, one population born and resident in Puno at an altitude of approximately 3900 m above sea level, and the other population of high-altitude ancestry but born in Tacna at a mean altitude of 560 m. The children in Puno are in general relatively smaller than those in Tacna. Individuals from both sexes in Puno weigh less than those in Tacna. In addition, the high-altitude children show smaller upper arm circumferences than the other group. These findings are consistent with the results of body weight comparisons, in the sense that nutritional conditions are much better in Tacna than in Puno. However, young males in Puno in some age classes, on the average, have slightly larger transverse diameters of the thorax, while no significant difference in growth pattern of transverse diameter of the thorax exists in the case of young females among the two groups. Except for the age of 18 years, the size of anterior-posterior chest diameter at each age class is not distinctly different between the two sexes and

neither between the groups under various environmental backgrounds. This study demonstrates that offspring of high altitude ancestry raised at low altitude express no substantial difference in thoracic measurements. Thus genetic adaptation to altitude contributes to similarities in the chest traits among the two Peruvian groups regardless of environmental contrasts.

Heritability estimates for anthropometric traits can give some evidence for genetic influence on phenotypic variation. The heritability estimate for sternal length in this high-altitude Peruvian population is 0.343, while that for sternal length in a sea level Belgian population is 0.787 (Susanne 1977). These values are consistent with the hypothesis that selection could have operated on sternal length, necessarily reducing the additive genetic variance. The heritability estimate for stature in this Aymara population is 0.509 while stature has a heritability estimate of 0.65 in a West African population (Roberts et al. 1978). These two values are not significantly different when the standard errors of the heritability estimates are taken into account. These results indicate that in both populations the stature shows moderately high heritability. The heritability estimate for weight is 0.400 and for upper arm circumference is 0.413 in this high altitude population. In contrast, the heritability estimate for weight is 0.625 in a sea level Belgian population and that for upper arm circumference is 0.458 (Susanne 1977). In comparing heritability estimates among populations, it should be taken into account that the heritability estimate is a function of the population and of environmental and genetic differences among populations. Thus, comparisons of different characters in the same population are more meaningful than the comparisons of traits between different populations. This is because variation in the order of coefficients obtained in a population gives more precise information on the relative genetic and environmental contributions to those traits.

In this study, the heritability estimates for the chest traits are lower than those for the traits reflecting overall body size. One possible interpretation of these findings is that selection has operated more strongly on chest dimensions than on overall body size, since selection would reduce additive genetic variation. As evidence for natural selection operating in the high-altitude Peruvians, Eckhardt and Dutt (1979) compared morphological changes in chest size between high- and low-altitude Andean populations. This study demonstrated that the thoracic volume was changed by over twenty per cent in a time interval of about 20,000 years at high altitude. Selection could explain the fast rate of evolutionary change when a population is confronted with harsh environmental conditions, in this case, hypoxia.

The direction and magnitude of selection in this study have been detected by a multivariate method. The results demonstrate that the standardized directional selection

gradient for stature is negative and lower, while standardized directional selection gradients for traits influencing thoracic volume are positive and higher. It can be inferred, therefore, that there has been weak selection for smaller stature as well as strong selection for larger volume of the chest in this population. The standardized variance selection gradient for stature is negative and relatively moderate, while that for the trait associated with depth of the chest is positive and relatively moderate. In turn, this might mean that phenotypic distributions of the traits under study, except for thoracic volume, are at equilibrium.

For traits representing body size, intermediate phenotypic values appear to have the highest relative fitness. Fisher (1930) showed theoretically that stabilizing selection depletes genetic variability in polygenic characters. However, in this population, the traits under stronger stabilizing selection show larger genetic variation than the traits under weaker stabilizing selection. In other words, body size traits, which are assumed to be of less adaptive significance, show reduction in the variance of the phenotypic distribution, indicating that they are less liable to be influenced by environmental factors. The finding that the traits describing thoracic volume are under stronger directional selection as well as under different degrees of magnitude for disruptive selection, can be explained. One possible mechanism of disruptive selection is the establishment of a polymorphism based either on developmental or on genetic factors. Selection for larger thoracic volume could have operated as the population mean has shifted toward large phenotypic variance. One further inference is that the traits of adaptive significance are still liable to be influenced by environmental factors inherent at high altitude.

Measurements of selection, along with the distinctions in morphology between high and low altitude Andean populations, along with the observed pattern of heritability estimates in this population, strongly support the hypothesis that evolutionary change by means of natural selection has taken place in this human population long exposed to an extreme environment.

APPENDIX A

ANTHROPOMETRIC TRAITS

WT : Weight

HT : Stature

STL : Sternal Length

APT : Anterior-Posterior Diameter Thorax (a measure of depth of chest)

TD : Transverse Diameter (breadth of chest at the marked level of the union of the third and fourth sternebrae)

TCN : Thoracic Circumference, Normal

UAC : Upper Arm Circumference

SS : Skinfold, Subscapular (a measure of trunk fat)

SIS : Skinfold, Supra-iliac (a measure of hip fat)

MAS : Skinfold, Mid-axillary

TS : Skinfold, Triceps (a measure of limb fat)

AH : Acromial Height (trunk length alone)

BD : Biacromial Diameter (breadth across the shoulders)

BID : Bi-iliac Diameter (breadth across the hips)

APM : Anterior-Posterior Diameter Manubrium (a measure of depth of the upper part of sternum)

APS : Anterior-Posterior Diameter Substernal (a measure of depth just below sternum)

TCFI : Thoracic Circumference, Forced Inspiration

TCFE : Thoracic Circumference, Forced Expiration

SCN : Substernal Circumference, Normal

SH : Sitting Height (lengths of trunk, neck and head)

APPENDIX B

AGE DISTRIBUTION OF THE CAMACANI AYMARA POPULATION

age class	age (yrs)	sampled #	
		males	females
1	0.0 - 1.3	10	7
2	1.4 - 2.6	11	12
3	2.7 - 3.9	8	10
4	4.0 - 4.9	8	10
5	5.0 - 5.9	7	8
6	6.0 - 6.9	8	9
7	7.0 - 7.9	12	13
8	8.0 - 8.9	9	12
9	9.0 - 9.9	15	9
10	10 - 10.9	19	11
11	11 - 11.9	15	5
12	12 - 12.9	12	8
13	13 - 13.9	24	19
14	14 - 14.9	17	13
15	15 - 15.9	30	14
16	16 - 16.9	17	7
17	17 - 17.9	15	8
18	18 - 18.9	13	7
19	19 - 19.9	9	2
20	20 - 24.9	23	24
21	25 - 29.9	17	16
22	30 - 34.9	12	12

23	35 - 39.9	11	28
24	40 - 44.9	24	10
25	45 - 49.9	19	25
26	50 - 54.9	16	17
27	55 - 59.9	17	15
28	60 - 64.9	12	15
29	65 - 69.9	11	6
30	70 - 74.9	6	5
31	75 - 84.9	8	4
32	85 - 100	7	4
	total #	442	365

APPENDIX C

PATTERNS OF AGE CHANGE

The following pages will show the age distributions of twenty anthropometric traits by sex.
Abbreviations for Y variables appear in Appendix A.
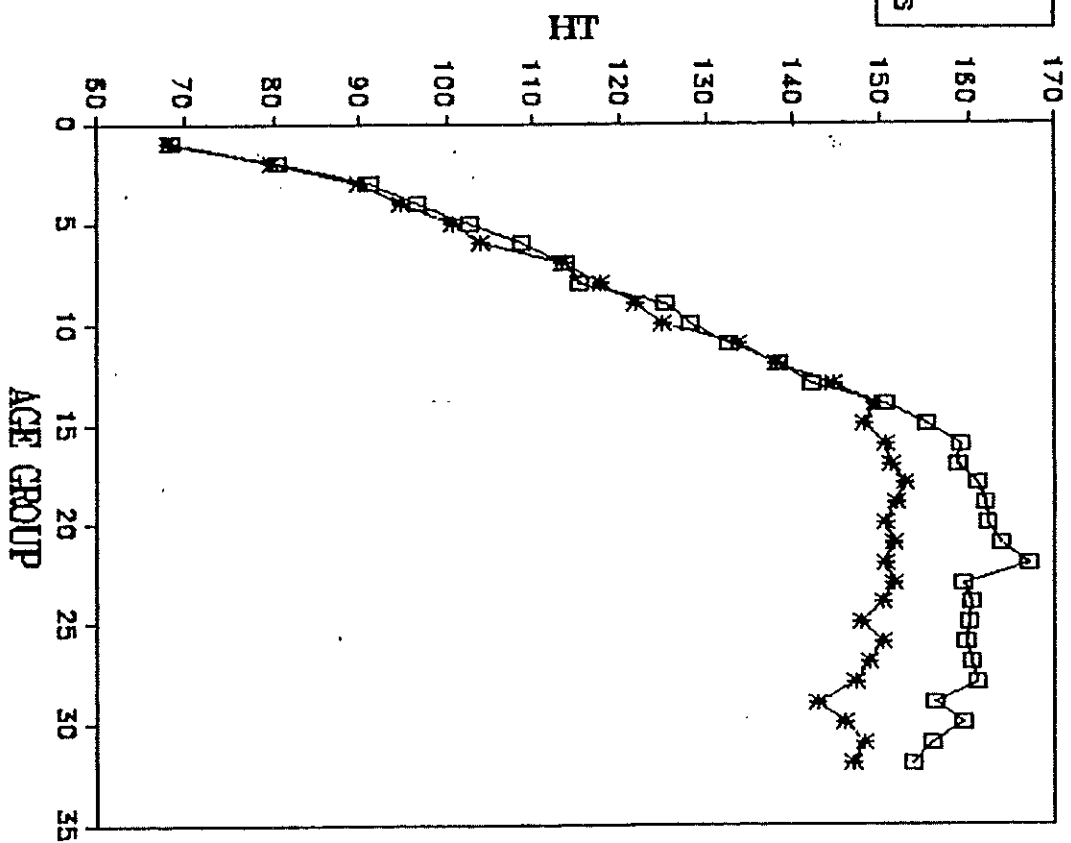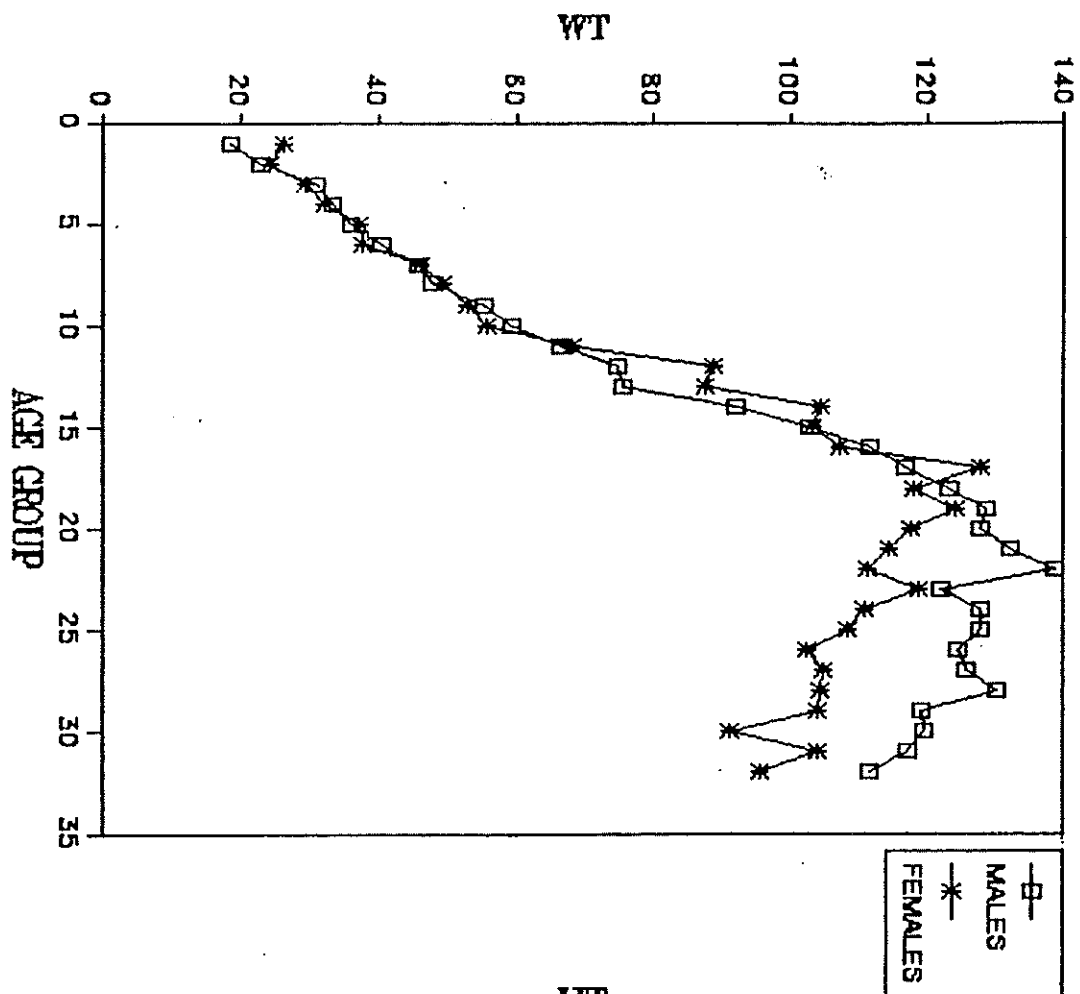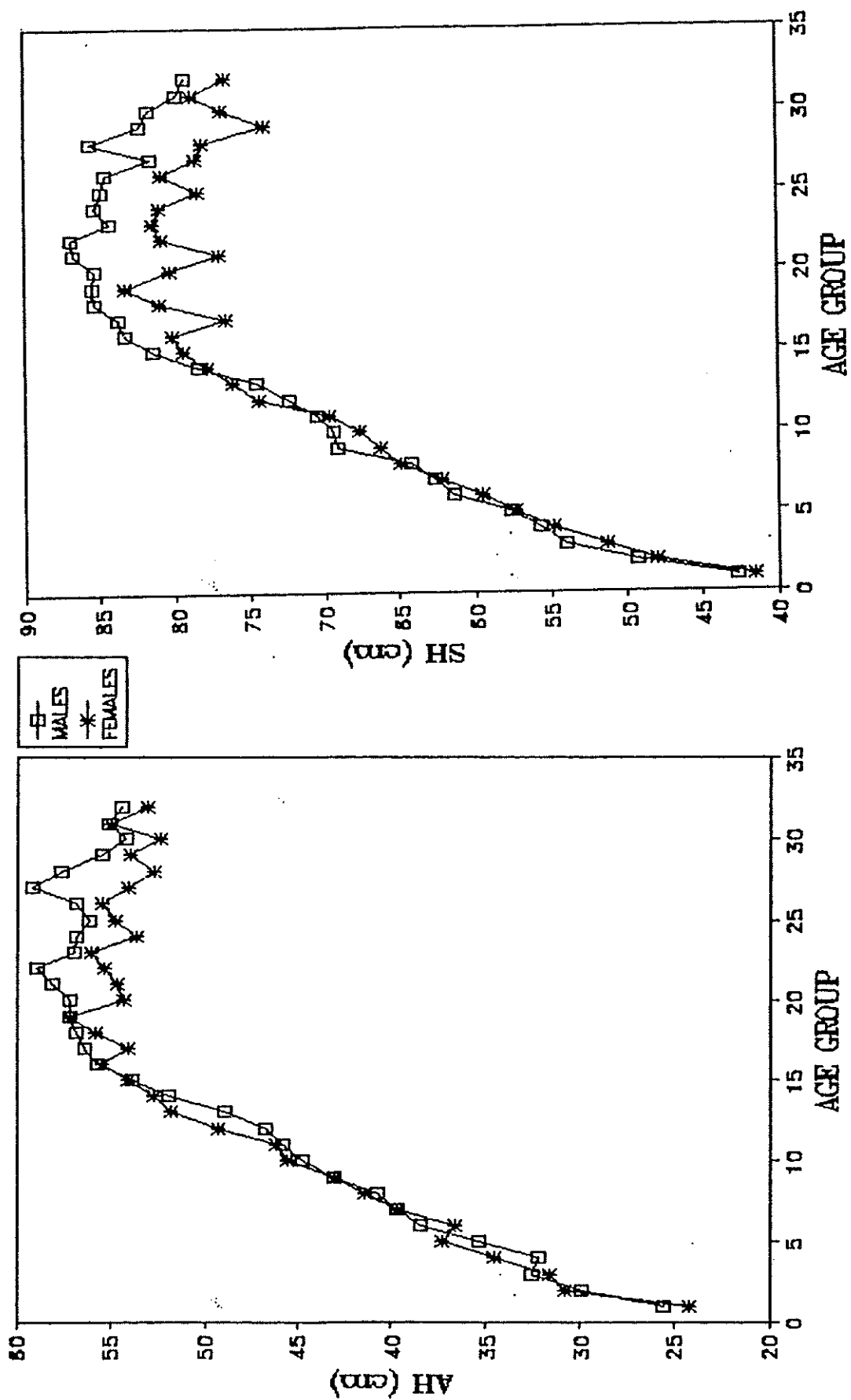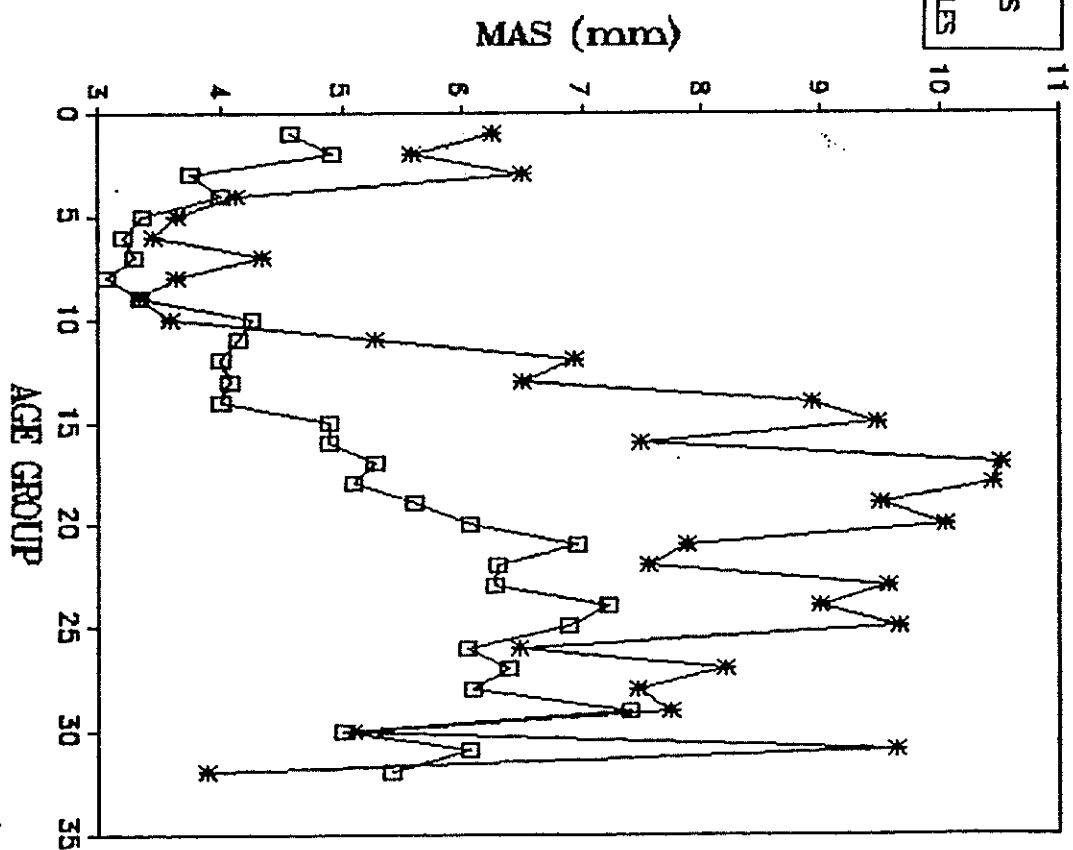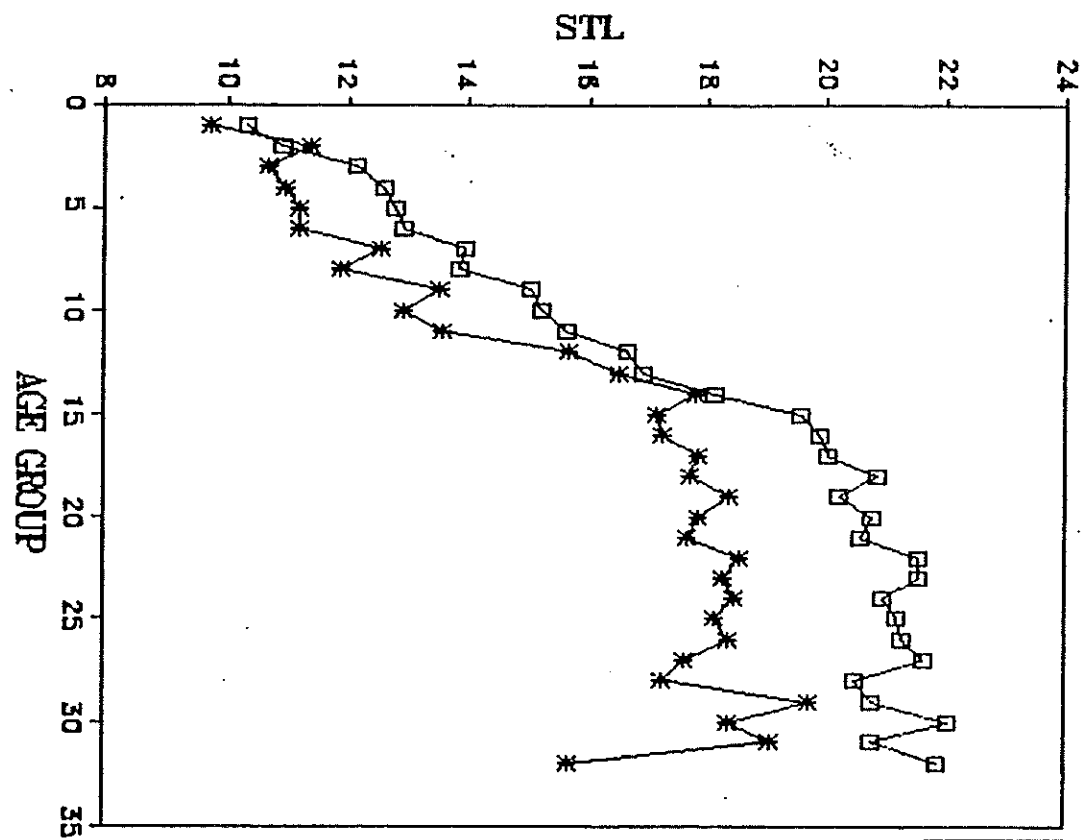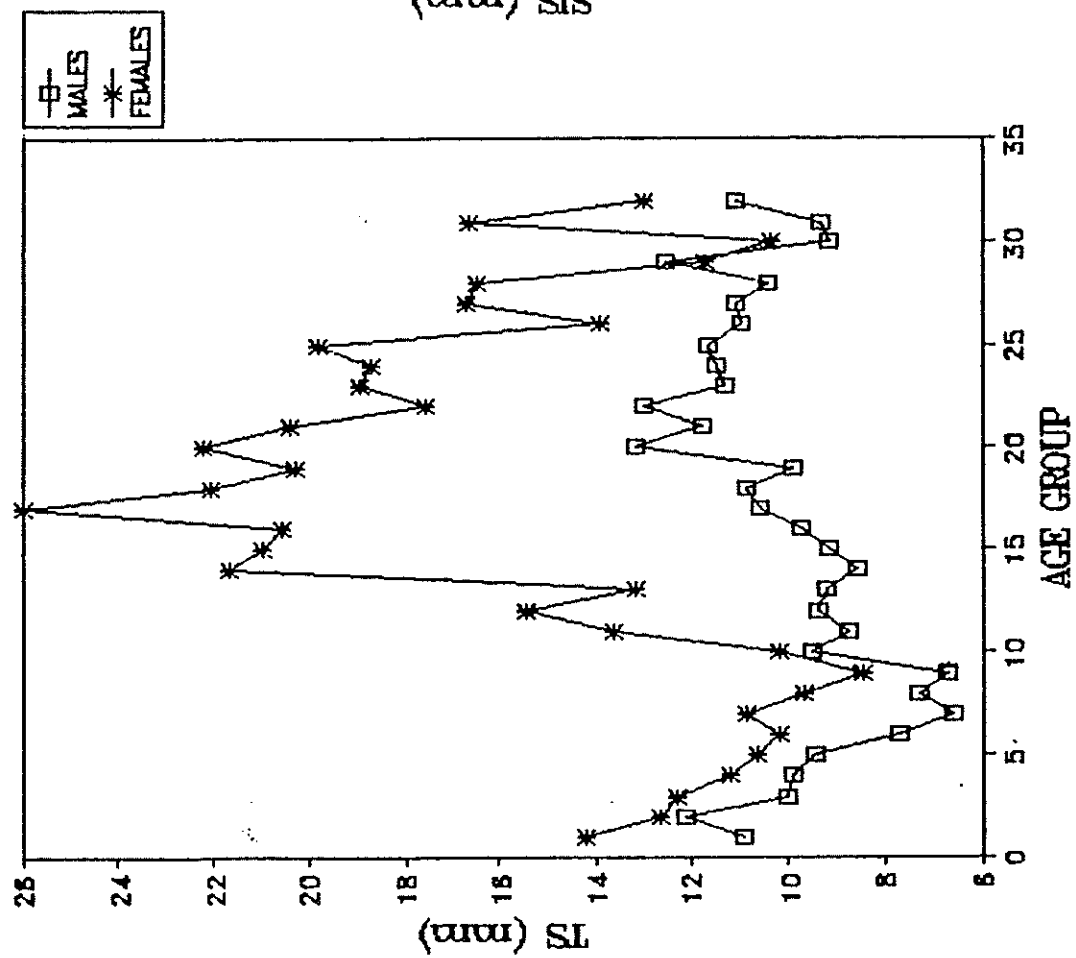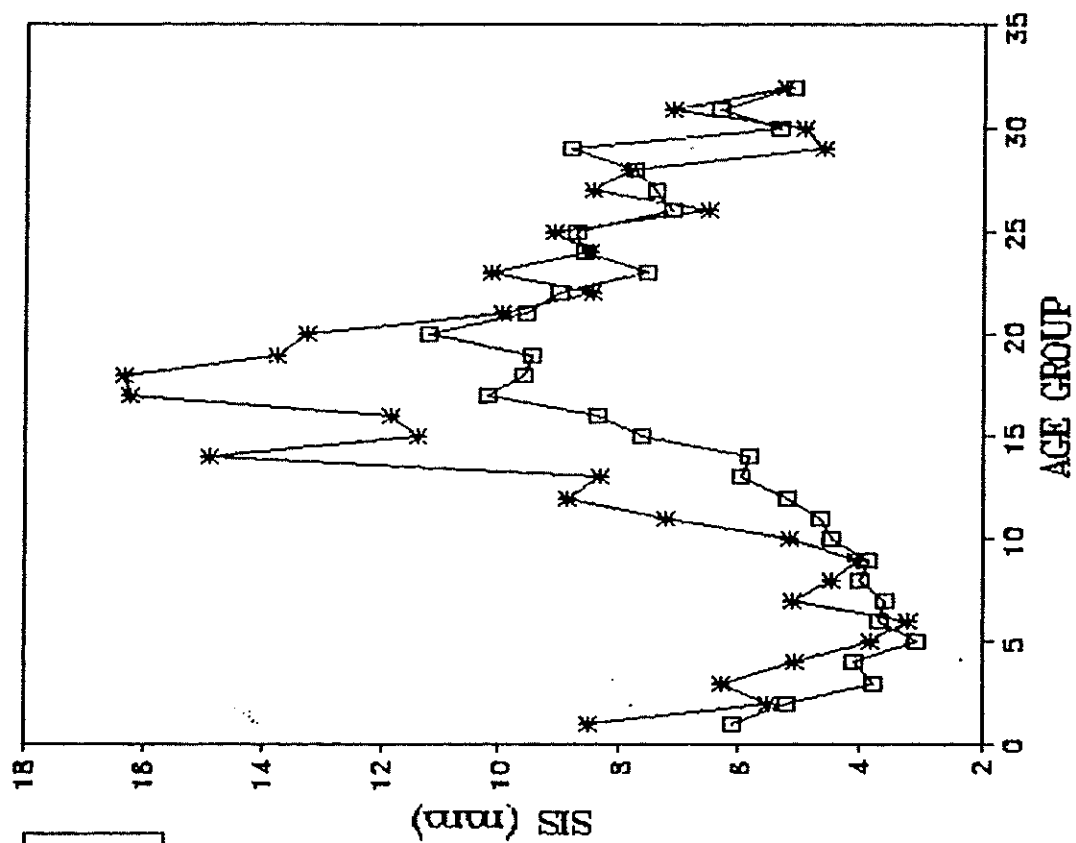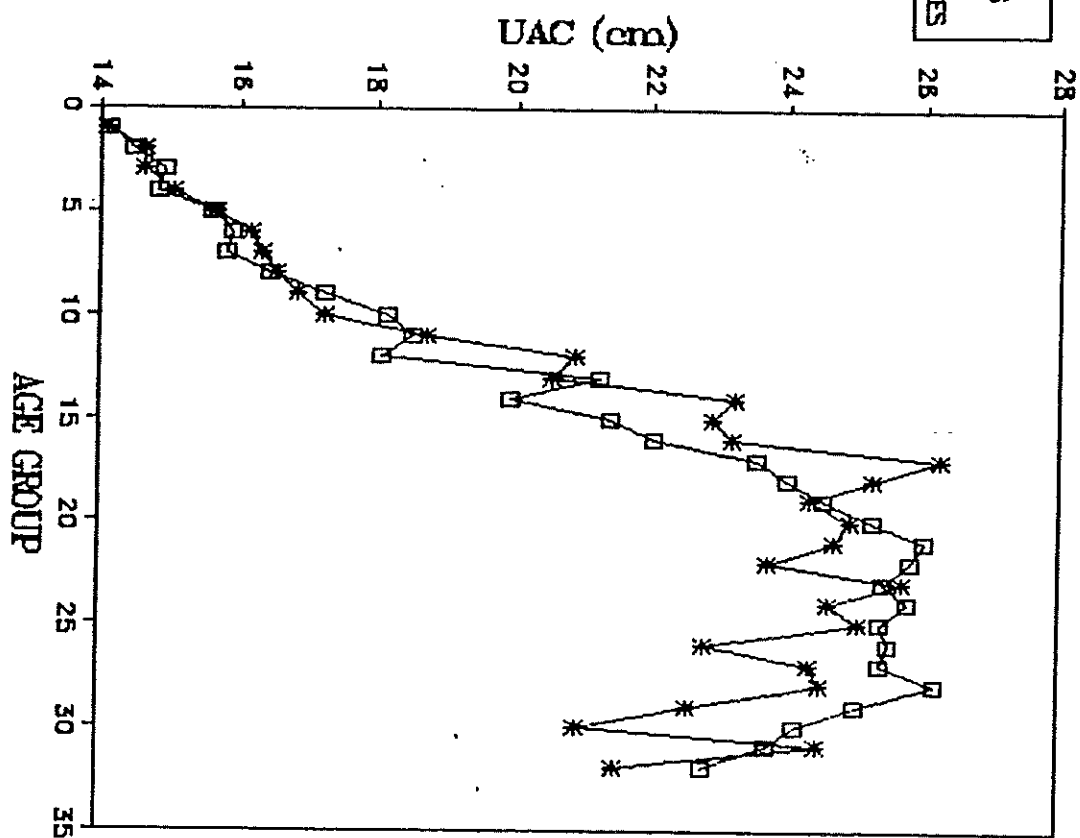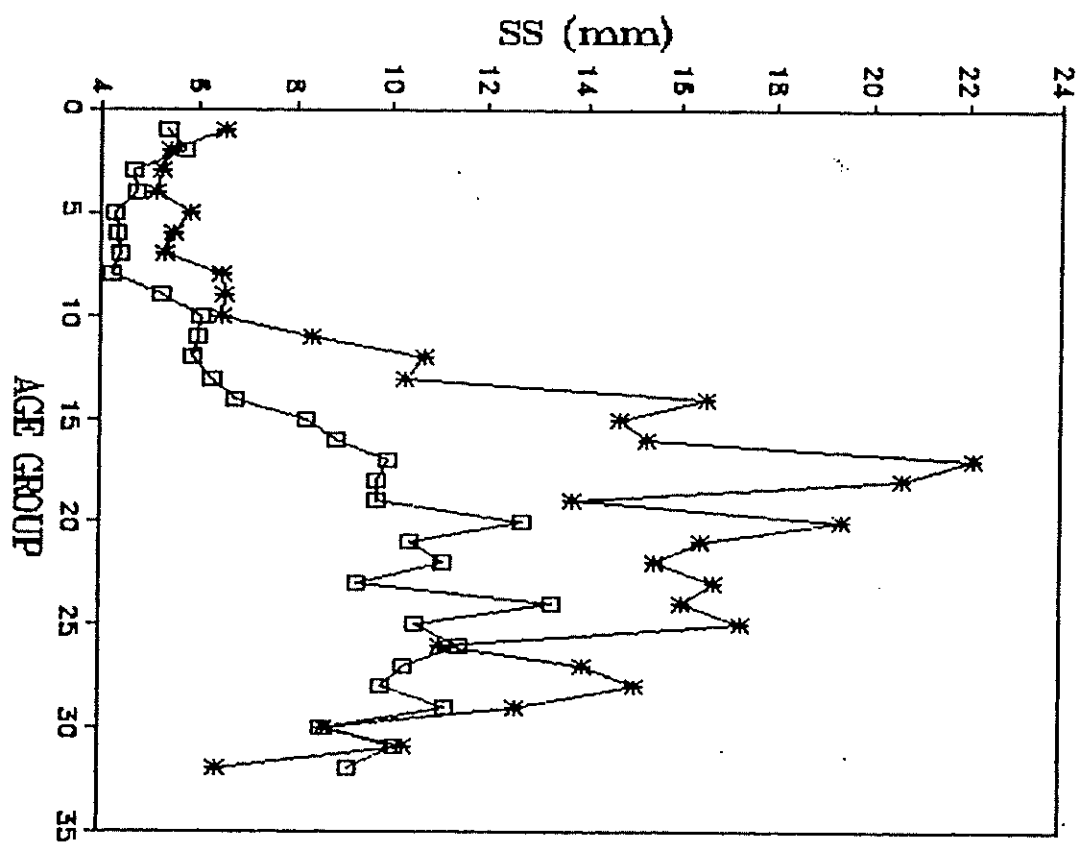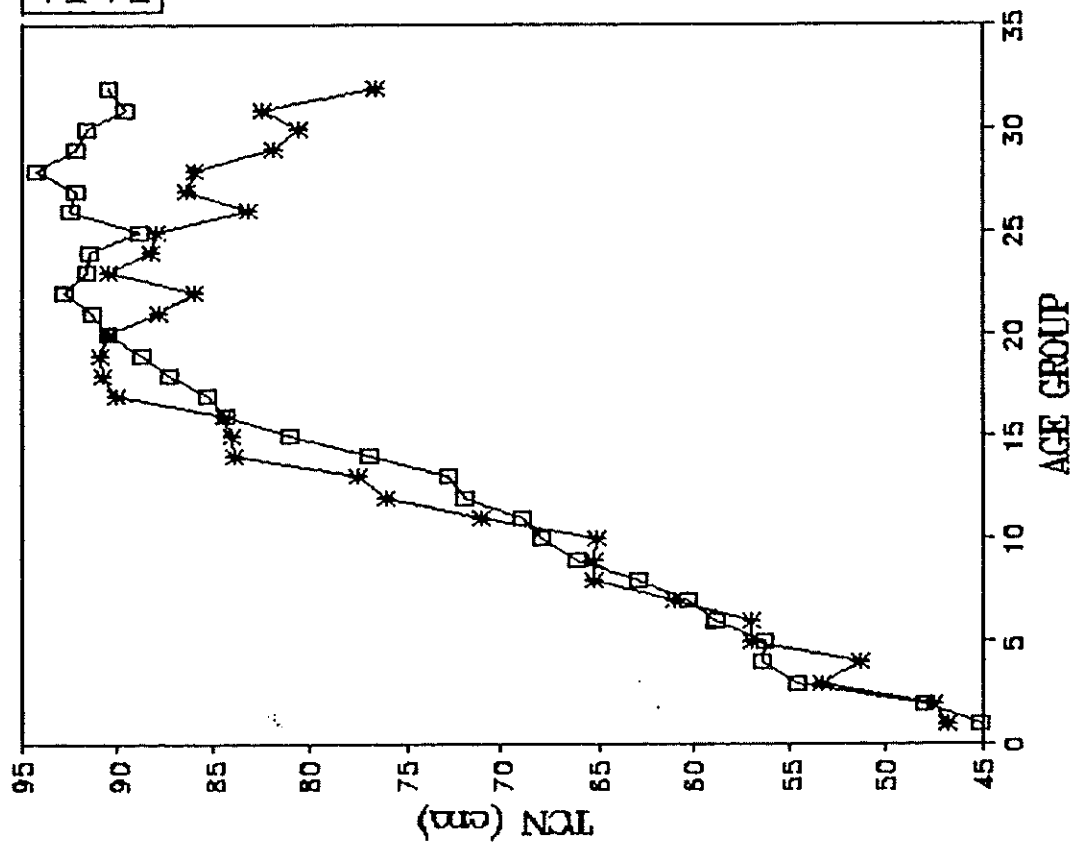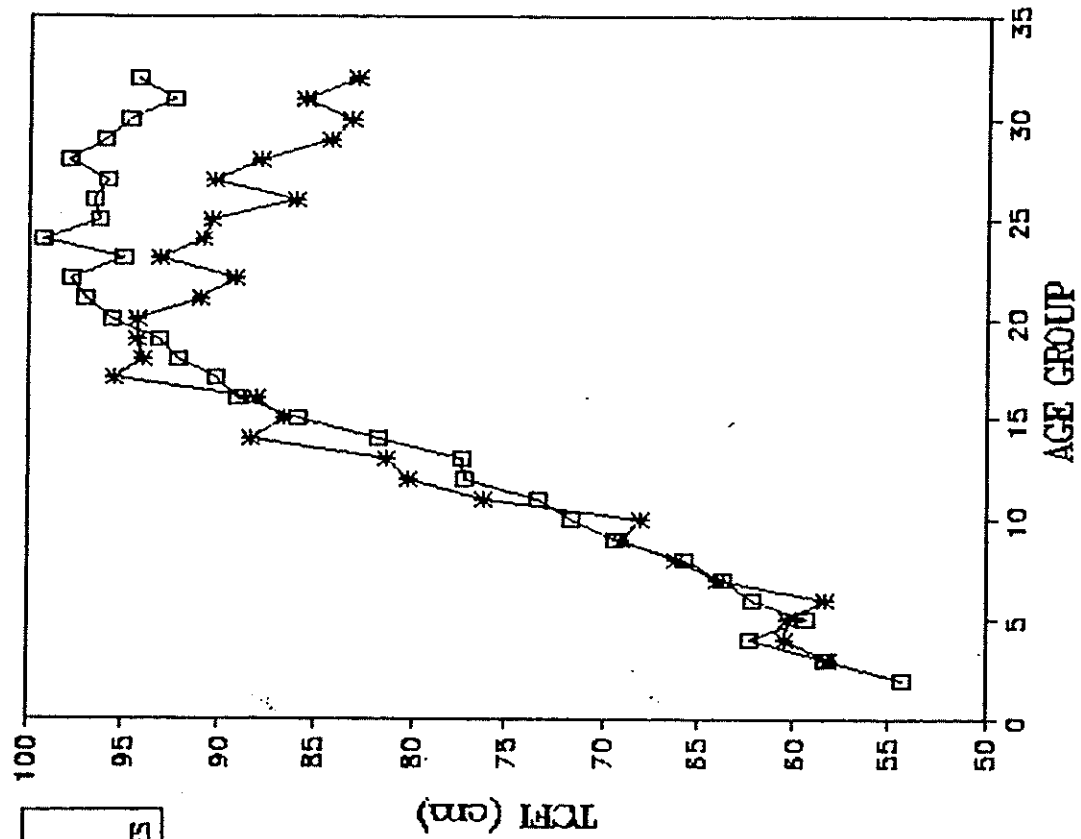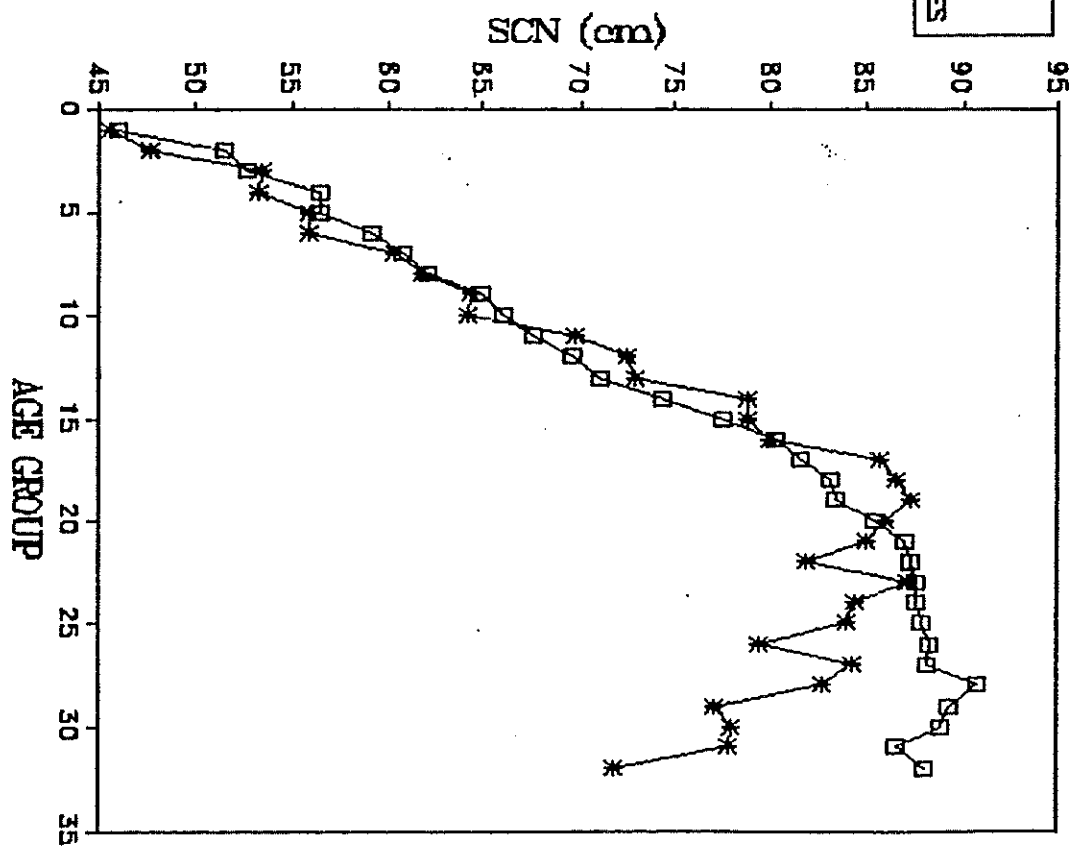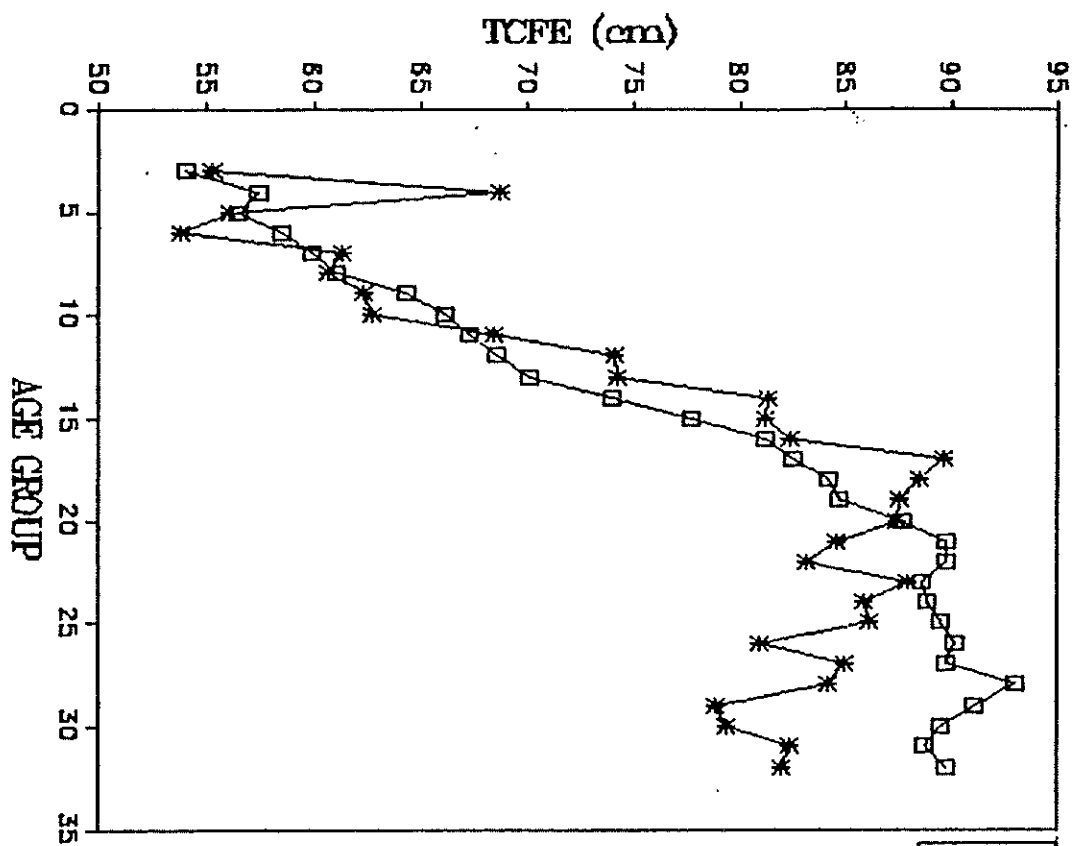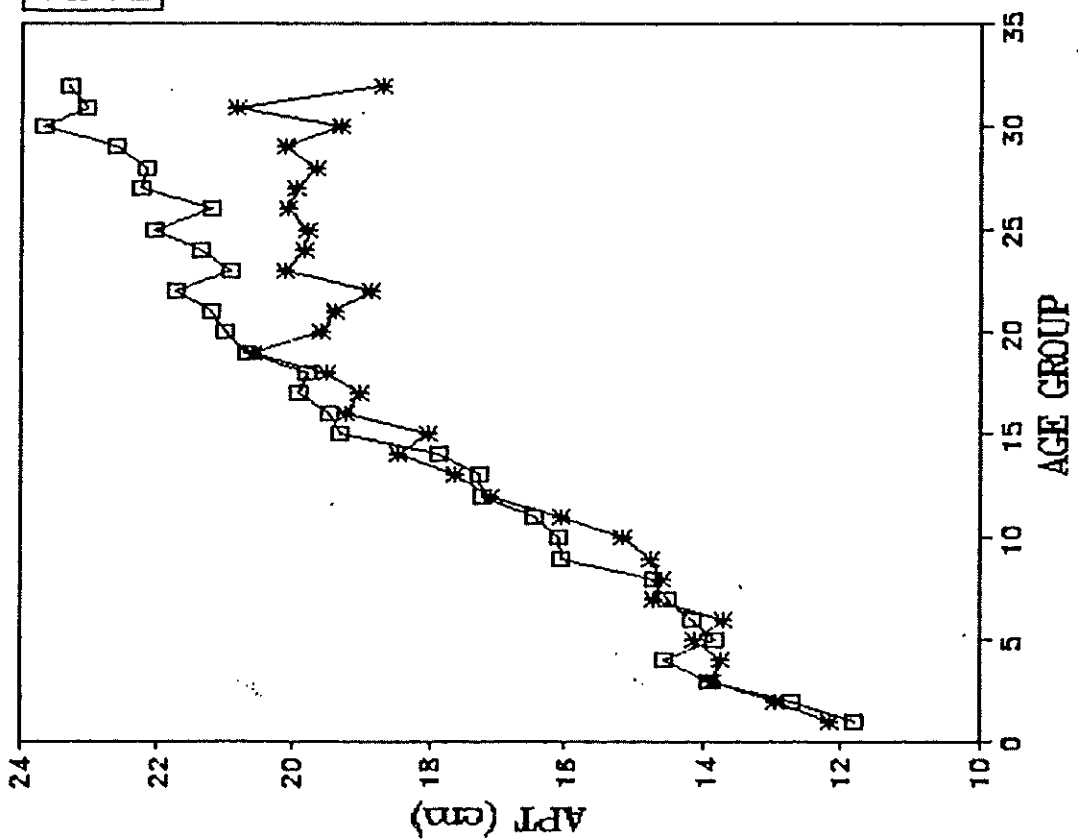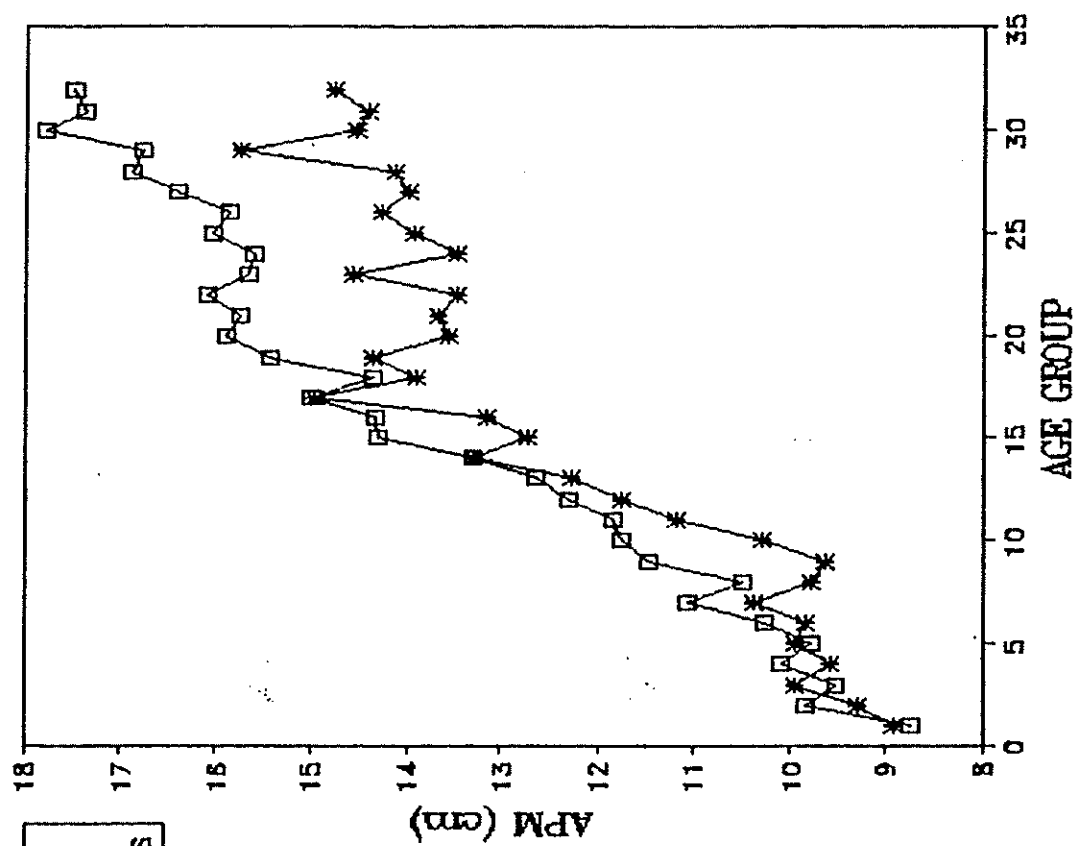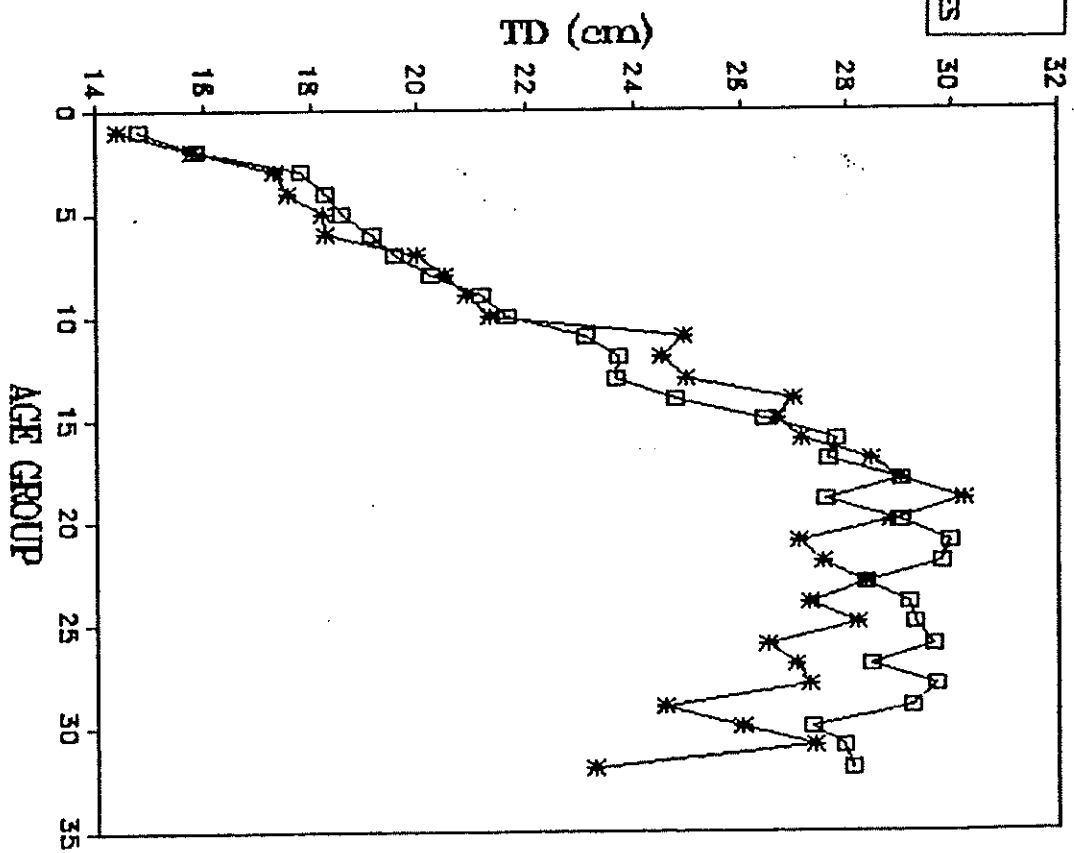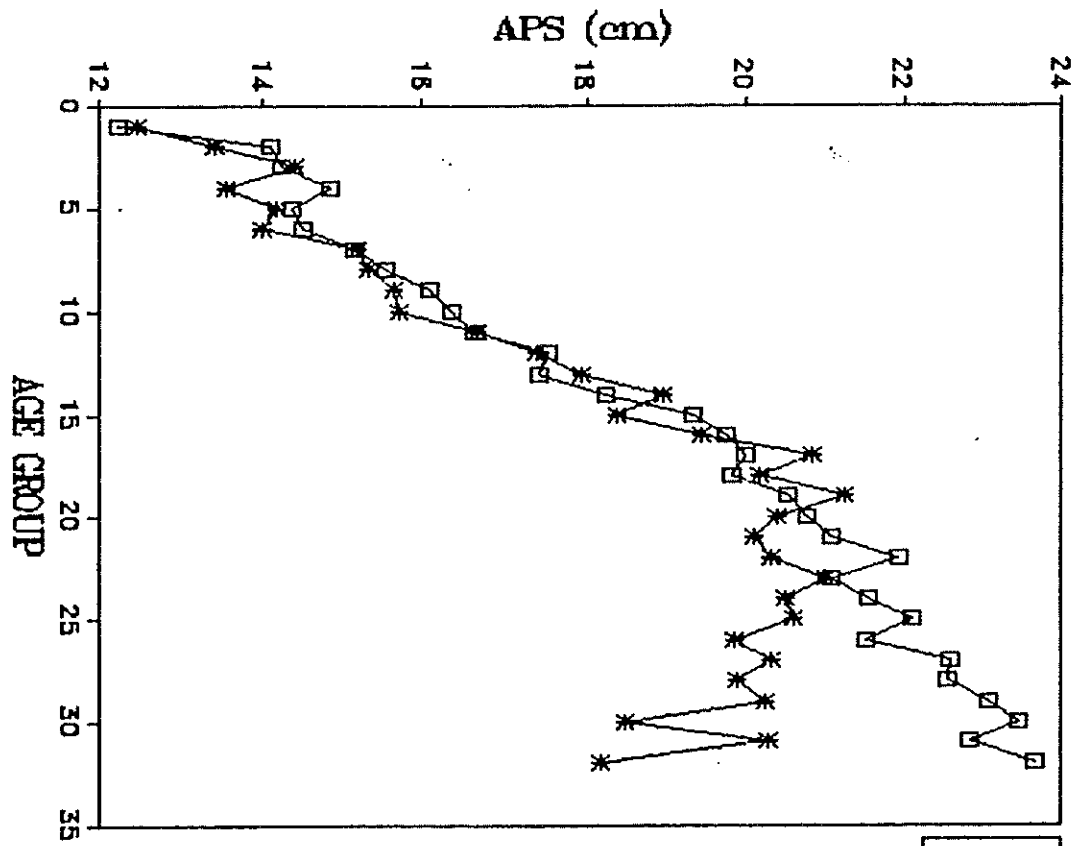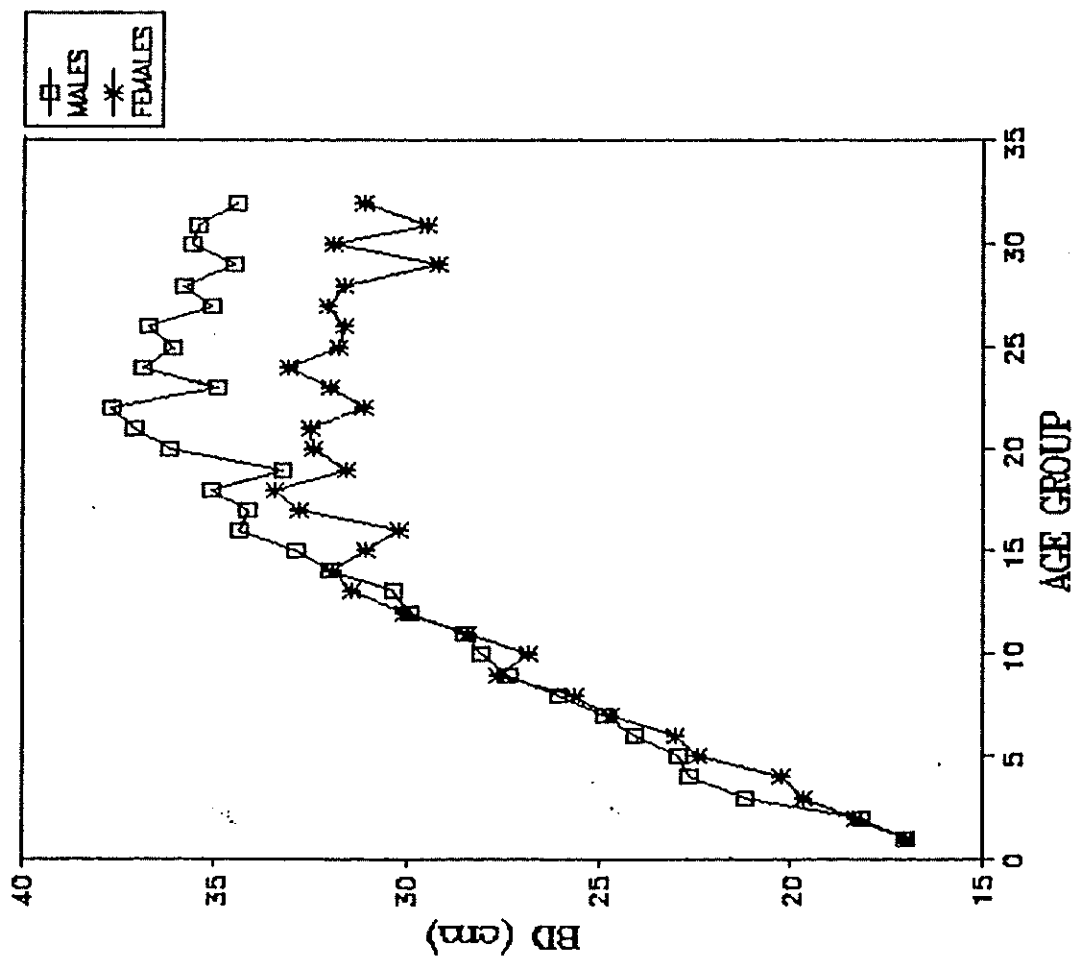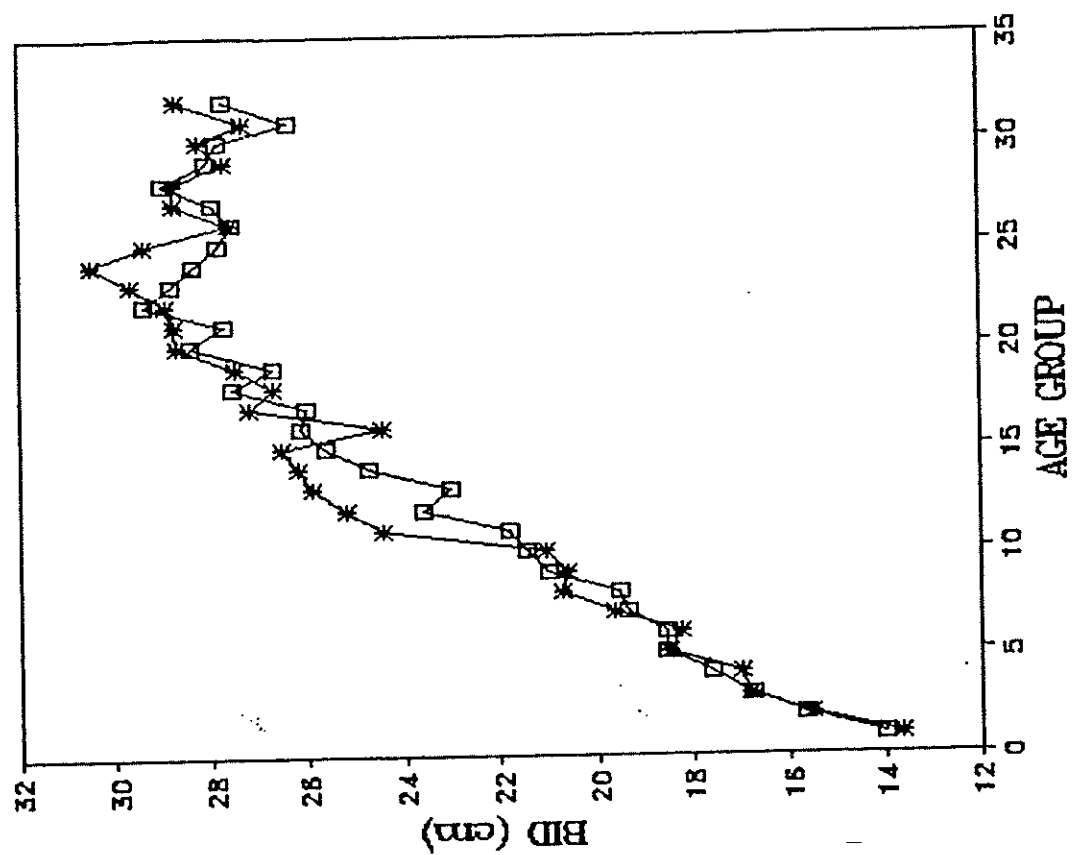
CHAPTER 8

COMPARISON OF GROWTH AND DEVELOPMENT IN
TWO PERUVIAN POPULATIONS OF HIGH ALTITUDE ANCESTRY

Terry Weary Melton

ABSTRACT

Analyzed here are twenty anthropometric measurements describing thoracic dimensions against a background of overall body size and nutritional status. The primary study sample comprises 218 subjects of high altitude ancestry, from six months through 19 years of age, who were born and raised at low altitude (560 m above sea level) in Tacna, Peru to parents who themselves had been born and raised in the region of Puno, Peru (3,900 m) and later migrated to Tacna. These subjects are compared with 443 subjects of similar ancestry who were born and raised in the Puno region.

Subjects from Tacna moderately surpass those from Puno in both stature and weight at all ages, which may reflect reduced nutritional, cold and hypoxic stresses at low altitude. The majority of thoracic dimensions in the Tacna group are at least as great as those from the Puno group. Tacna males are at least as large as Puno males for two of twelve traits related to thoracic size and larger than Puno males for eight more. Tacna males exceed Puno males in all measures of thoracic circumference. There are no differences in transverse thoracic diameters or AP diameters at the manubrium or substernal levels. Females from Tacna are at least as big as Puno females for five traits representing thoracic growth and larger for five more. Sternal height is consistently greater for both males and females from Tacna over 4 years of age. These findings provide support for the existence of a genetic component in the growth patterns of the thorax for Andean populations.

INTRODUCTION

Growth, Genetics, and Environment

Rate of growth and terminal points of growth in all organisms are determined by both heredity and environment. A question central to all studies of growth and development is: given the genetic variability present in human populations and the diversity of environments present, what will be the relative effects of each in determining the limits of bodily size?

Interaction of heredity and environment contributes to limiting or enhancing the potential for growth, as noted by Goldstein (1943):

> The limits to bodily change in any people largely
> depend... on an environment conducive to the
> attainment of the optimum realization of the gene-
> tic potential among the individuals comprising the
> group. (p. 22)

Stressful environments for infants and children are well known to contribute to slow-down of growth and eventual limitation of size, with the most extreme example being that of the "failure-to-thrive" syndrome seen in abused children. Environments with a paucity of nourishment and psychosocial interaction, extremes of climatic conditions, or increased incidence of disease will adversely affect the children inhabiting them. For example, during periods of acute respiratory illness, children grow an average of one centimeter less per year than during corresponding periods without illness (Rogers 1984). Catchup growth occurs in children when a period of undernutrition is followed by a period when nutrition is adequate, and is even accelerated compared to normal growth (Tanner 1986).

While environment influences growth, so too does the genetic potential present in each individual which is predetermined by segregation of genes inherited from parents. Quantitative genetic analysis shows high correlations between relatives for many traits which display continuous variation, including those such as weight, stature, and other linear and volumetric indicators of growth. In fact, growth itself could be considered a quantitative trait, whose total variance in a population is composed of the sum of genetic variance and environmental variance, as delineated by Falconer (1989).

Separating out the relative effects of environment and heredity can help determine whether natural selection has occurred in human populations which have adapted to extremely stressful habitats. Developmental adaptation, defined as changes in the morphology or physiology of an organism driven by environmental conditions during the growth period, would not cause changes in the genotype of the population, and would therefore not be inherited. Selective forces operating in a population for many generations, however, would alter the genotype for multilocus traits, and this effect would be apparent in the phenotypes of offspring removed from the stressful environment and reared elsewhere.

The populations of southern Peru present a unique opportunity to examine the relative effects of genes and environment on skeletally-related traits, because of long-term human habitation of the Andean highlands, which present the people living there with extreme environmental challenges. This study compares two groups of children and adolescents who have been exposed to very different environments, but have a common ancestry.

The Environment and Population of Highland Peru

Archeologists postulate that the Peruvian Andes have been populated by Amerindians for between 10,000 and 20,000 years (Steward and Faron1959). A population wave spreading into South America along the Pacific coast would have encountered an environment with unique geographical conditions, as described by Jenks (1956). The Corderillera Occidental is the series of high ranges on the western coast of Peru, which face the Pacific Ocean. The Titicaca Basin, an area at high altitude surrounding Lake Titicaca, separates the Corderillera range into the Occidental and Oriental ranges at Peru's southernmost border. Central Peru boasts the greatest elevations of the Andean range, with highest peaks at 6,800 m above sea level, and mean altitudes of 4,700 m. Peaks of southern Peru reach comparable elevations. Climatic conditions are largely determined by these mountains, which are high enough to create polar climates in spite of the tropical latitudes (Eidt 1969). High altitude upland basins, termed the altiplano, exist between high ranges and are extremely arid, as the mountains prevent moisture-laden air driven from the Pacific from entering the interior of the continent. The altiplano has significant diurnal variation of temperatures, with mean range of maximum and minimum temperatures of over 20 degrees Celsius (Thomas and Winterhalder 1976). Annual seasonal temperature fluctuation, however, is not great, due to amelioration by the tropical latitude.

By far the most pervasive stress of the altiplano is hypoxia. Barometric pressure decreases with altitude, so with higher elevation there is reduced density of oxygen. At 3,500 m above sea level, the air contains 35% less oxygen, an environmental condition sufficient to cause illness in those not acclimatized to such altitude. Hypoxia can induce fatigue, shortness of breath, headache, nausea, vomiting, and mental confusion at high altitudes, and failure to respond by returning to lower altitudes can lead to rapid worsening of symptoms and even death (Mongé and Mongé 1966).

The altiplano is peopled by highland natives whose culture rests on subsistence agriculture and herding. Crops consist of potatoes, other tubers, barley, beans, oats, rye, quinoa and canihua, onions and other vegetables, which comprise the major part of the diet with supplementation with meat from cattle, llamas, alpacas, sheep, guinea pigs, some domestic

fowl and fish (Collins 1988, Picón-Reátegui 1976). Soil conditions of the altiplano are poor due to inhibition of organic decomposition by the aridity and cold temperatures, and periods of drought cause crop failure periodically (Collins 1988). Limitations on travel due to poor roads and bad weather effectively isolate these people from outside sources of goods and services.

The native highlanders of southern Peru, therefore, experience stresses related to their environment every day. Cold temperatures, low humidity, hypoxia, and marginally adequate food supplies are facts of their existence, but they are uniquely adapted to these living conditions. Their adaptations, evident in unusual skeletal morphology, are discussed in the review of previous studies.

The Migrant Population of Lowland Peru

Coastal Peru has one of the driest climates in the world (Erickson et al. 1965). Irrigation is possible, however, with water from the Andes. Almost all the nation's commercial agriculture is centered in fertile alluvial valleys along the coast. Highly mechanized plantations grow sugar, coffee, rice and cotton in tropical temperatures of the northern coast, and cotton, fruit, truck produce and tubers thrive in the semitropical southern areas. The successful cultivation of crops there contrasts with the difficult and unpredictable agricultural conditions of the sierra and altiplano.

With the growth of a diversified industrialized economy in Peru since the beginning of the twentieth century, there have been accelerated population growth and substantial internal migration from rural to urban areas (Maletta and Bardales 1985, Cotlear et al. 1987, Collins 1988, Malmberg 1988). DeJong and Gardner (1981) summarize the major motives related to migration in developing nations. The primary reason for a family move is economic, followed by desire to maintain ties with extended family which has previously migrated. According to Malmberg (1988), in 1940 one-third of Peru's population lived in its cities, whereas today two-thirds of the nation's population lives in urban environments. Most of Peru's cities are found in the coastal area. Because of falling death rates and higher birth rates associated with better living conditions, Peru's population growth has been rapid in the last five decades.

The traditional socioeconomic structure in rural areas has been disrupted by changing economic relationships between rural and urban areas (Malmberg 1988). The earliest labor migration linked peasant communities with the outside world and resulted in development of a local market economy and loss of local self-sufficiency. Needs for cash and increased awareness of goods and services available outside the rural economy led to desire to supplement individual agricultural production with wage incomes. Dependence on traditional forms of

family support in rural areas became less certain, especially in areas where quantity of subsistence crops was unpredictable. Large losses in crops occurred several years in a row in the early 1940s and late 1950s, forcing migration of many families seeking sources of certain income elsewhere (Collins 1988).

While areas of the altiplano, such as Puno, near Lake Titicaca, lost residents for the reasons above, coastal cities such as Tacna, in southern Peru, gained residents. For example, between the censuses of 1961 and 1972, the province of Puno, a district of the larger Department of Puno, had a net loss of 22,808 individuals whereas the province of Tacna, within the Department of Tacna, gained a net total of 25,842 people (Maletta and Bardales 1985). These statistics are characteristic of the net losses of all rural communities and net gains of larger, more prosperous towns and cities. In fact, the total population of Peru was reported to be 17.03 million in 1981, and Lima, the capital, showed a net gain of 1.23 million people in the years 1961-1972.

The migrant subpopulations of these cities provide a source for determining the effects of change of environment on the patterns of growth and development in offspring who are born and reared in the new location. For those families migrating from high altitude altiplano environments to the coastal low altitude cities, a change in lifestyle is inevitable. The offspring of these families will experience an environment lacking the stresses that were present for their parents, but would retain the parental genes which allowed adaptation to the highland environment.

Objectives of the Study

Two populations were sampled, a group of children and adolescents from the high altitude area of southern Peru, and a similar group from the city of Tacna, near the Pacific coast. These individuals have a common ancestry: all parents of these subjects were born and raised at high altitude. The parents of the Tacna group are first generation migrants from high altitude. Anthropometric measures were taken for twenty skeletally-related traits, with emphasis on those which define thoracic development and growth. Analysis was performed to determine if significant differences were present in the trait measurements for the groups. Results could aid in discriminating whether the observed phenotypes are shaped by short term developmental adaptation or by genotypes determined by natural selection.

The next section will review studies pertaining to the unique skeletal morphology of Andean groups.

REVIEW OF PREVIOUS STUDIES

Growth Patterns of High Altitude Peruvians

The growth patterns of high altitude populations have been documented extensively, as have the physiological processes which contribute to adaptation to hypoxia. Controversy exists as to whether the unique morphology and physiology have a substantial genetic causation or are a novel response to the environment within each generation. Various studies support each hypothesis, and a synthesis of these papers can provide an idea of the complexity of factors involved.

This section will be confined to describing growth and physiology of high altitude populations, and the following two sections will separate studies into those which support a developmental causation and those which support a genetic causation. The final section will discuss studies pertaining to migration of groups, and effects of migration on phenotypes.

As early as 1870, the large chest sizes of high altitude Peruvians were documented in the scientific literature (Forbes 1870). Hurtado (1932a) studied 950 males at 4,000 m above sea level and observed that there was increased thoracic development relative to height. He observed clubbing of the fingers, a condition seen in individuals with chronic low oxygen absorption, and noted at autopsies that lung tissue from high altitude natives showed increased capacity and dilated capillaries, implying that there was increased surface area for diffusion of respiratory gases.

With the advent of a large multidisciplinary study of Peruvian populations at high altitude in the 1960s (Baker and Little 1976), data on growth and physiology became abundant. Cross-sectional and longitudinal studies of children and adults in Nuñoa, at 4,000 m, recorded unusual growth patterns, characterized by lack of a well-defined growth spurt for males, a late and poorly-defined growth spurt for females, a long period of overall body growth, and larger chest sizes at all ages than those of comparable low altitude populations (Baker 1969). Later eruption of teeth and delayed motor development by U. S. standards were observed. Infant birth weights were lower than those at sea level, and an increased ratio of male to female births and increased mortality of females throughout the growth period were also seen.

Frisancho and Baker (1970) studied rural and urban groups of children within Nuñoa and found that boys had chest circumferences which were 12% and 15% greater on average than comparable American and low altitude Peruvian samples, respectively. While stature in both the rural and urban groups developed to the same endpoint, the urban group was heavier, with increased subcutaneous fat, pointing to the role of nutrition in determining size.

A study of 150 Quechua boys (Frisancho 1969) showed that compared to low altitude Peruvians, there was increased chest circumference in spite of smaller stature, and higher values of forced vital capacity. At low altitude, chest circumference was only slightly correlated with forced expiratory volume, whereas at high altitude it was highly correlated.

Velasquez (1976) summarized pulmonary function and oxygen transport in Nuñoa natives. Ventilatory capacity is greater at high altitude, as is total lung capacity. Highlanders have increased hemoglobin concentrations to transport the larger gas volumes to tissues with the same degree of efficiency seen in lowlanders. The affinity of hemoglobin for oxygen may be lower, which speeds dissociation of hemoglobin and oxygen and allows low oxygen pressures to drive oxygen into the tissues with increased success.

Menarche is later for high altitude girls, with a mean age of 13.58 years compared to 11.58 years for low altitude girls (Donayre 1966). Since menarche is correlated with bone maturation, this result is not surprising in light of the protracted growth period for high altitude children.

Studies Which Suggest Developmental Causation

Peruvian high altitude children grow more slowly, mature later, and are smaller than their low altitude cohorts, while having larger chest sizes relative to stature. Causing these characteristics is a certainly a blend of environmental factors (including cold, undernutrition, and hypoxia) and genetic factors. Some authors correlate the characteristics more strongly with the pervasive environmental conditions, however, while others equivocate, leaning towards primary environmental influences and not ruling out genetic causation.

In a comparison of genetically similar groups of Quechua children from Pamashto (980 m) and Ondores (4,150 m), Frisancho et al. (1975) found the growth of the lowland children markedly delayed compared to that of the highland children. Skinfold measures and upper arm circumferences indicated that the low altitude group had less adequate caloric intake over a long period of time, which might be due to a current deterioration of the local economy and associated poverty. These groups had previously been determined to have similar ABO and Rh group frequencies, therefore were considered to be of similar genetic origins. The conclusion drawn from this study was that the differences between the groups were more attributable to nutrition limited by socioeconomic conditions, because if the characteristic growth were genetically determined, the two groups would have been more similar. Highland children significantly exceeded lowland children in measures of chest circumference, in addition to being heavier and taller. Although these groups are similar in terms of blood group genotypes,

however, it cannot be assumed that they have similar genotypes at other loci, including those which might influence chest development. In addition, it is more likely that genetic effects will be evident in the total potential for growth rather than in limitations on growth, as it is well documented that nutritional deficits will limit growth in any population.

Lahiri et al. (1976) concluded from studies of respiration in high and low altitude subjects and migrants to both high and low altitude environments in Peru that adaptation to hypoxia was exclusively developmental. Neonates born at high altitude of highlander parents showed similar responses to hypoxia to those of lowlander neonates studied under hypoxic conditions. Patterns of response to hypoxia in highlanders changed with age, suggesting that adaptation is acquired throughout childhood rather than innate. Migrants to high altitude acclimatized to the hypoxia, a situation previously known to occur. Sample sizes were small, with 20 neonates each at low and high altitudes, 43 children up to age 12, and 58 adolescents studied, and the subjects were from diverse genetic sources. Moreover, these results do not exclude the possibility that selection for large chest size has occurred in high altitude populations; no anthropometric measures were gathered.

Leonard (1989) compared measures of height and weight over a period of twenty years in high altitude groups in Nuñoa. Results showed that increasing family incomes are resulting in better nutrition and subsequent increases in weight and stature, pointing to major influences of nutrition which surpass the effects of hypoxia in determining growth. Stature and weight, in this study, appear to have substantial plasticity, eliminating the possibility that genetic effects are responsible for the small stature characteristically seen.

Stinson and Frisancho (1978) report on the body proportions of Quechua children from different altitudes (Pamashto and Ondores, see above) with similar ABO and Rh blood group frequencies. Body proportions were different in the groups: although the highland children showed greater stature and weight, they had shorter legs relative to stature, and shorter arms relative to stature and sitting height. The authors conclude that climate, which is cold and dry at high altitude, and hot and humid at low altitude are determinants of these characteristics because of the relationships between body area and heat loss in different climates. Although this can logically be concluded to be a direct environmental effect on growth, these differences may be due to genetic differences caused by selective effects.

Studies Suggesting a Genetic Causation

Other researchers find the hypothesis of a genetic causation for the unique skeletal morphology of Andeans to be more compatible with their results. Arnaud et al. (1985) examined the erythrocyte metabolism of Aymara and Quechua populations in Bolivia. Quechuas, which comprise the largest ethnic group retaining a language of its own in South America, are less territorially isolated and more genetically heterogeneous, and are descended from the Incan culture. The Aymaras, resident in the more remote altiplano regions, are a smaller, more isolated group descended from the earliest known Andean natives (Vellard 1976). At high altitude, differences in intensity of metabolic response to hypoxia were noted between the two groups. Quechuas, removed to low altitude, showed quickly reversible responses in adaptive phenomena much as any lowlanders would, whereas the Aymaras retained most of the hematological characteristics seen at high altitude. Arnaud et al. conclude this group has been isolated for generations at high altitude and consequently has undergone natural selection for adaptive physiological mechanisms to compensate for hypoxic stress.

An examination of respiratory function in Peruvian Quechuas by Boyce et al. (1974) selected males living at high and low altitude and migrants between those areas. High altitude subjects have higher lung volumes and ratios, and lower rates of decline of these with age. While migrants from high to low altitude come to resemble coastal residents in their respiratory characteristics, Quechuas resident at both high and low altitude have high expiratory volumes and vital capacities compared to other world populations. This study implies that the Quechuas have undergone some selection for larger chest sizes and consequently greater respiratory volumes as a result of being resident at high altitude for thousands of years.

Beall et al. (1977) looked at growth in height, weight and two thoracic diameters in three groups of Peruvian children. Tambo-1 consisted of those born at less than 3,100 m above sea level whose parents were of low altitude ancestry. Tambo-2 included those born at less than 3,100 m whose parents were of high altitude ancestry, and Nuñoa children were born at high altitude (4,000 m) and had parents of the same origins. This study found that altitude had a significant effect on the growth of height and weight of the groups, with the Nuñoa group being generally shorter and lighter. Chest growth was not correlated with altitude-related differences in height and weight, indicating that chest growth may be under different genetic control than height and weight. When measured relative to stature, the chest of the Nuñoa group was larger than that of the lowlanders, but age by age the chest of the lowlander of the Tambo-2 group was somewhat larger than that of the highlander. Significantly, the adult

chest sizes were similar. These results support the hypothesis that chest size may be large due to inherited differences, not exclusively as a developmental response to hypoxia.

Eckhardt and his colleagues (1985) quantified the amount of additive genetic variance present in twenty anthropometric traits for the population of Camacani, an altiplano village near Lake Titicaca. Estimates of heritability were calculated for traits related to thoracic skeletal dimensions (Kramer 1980 and this volume, Ahn 1986 and this volume), and nutritional status (Vandemark 1985 and this volume). While stature for this group had a heritability of 0.509, comparable to that of a Belgian sea-level population of between 0.5 and 0.6 (Susanne, 1977), sternal length had a heritability of 0.343, less than half that of 0.79 in the Belgian group. This low additive genetic variance is consistent with the explanation that directional selection has occurred in the Andean group, reducing the additive genetic variance as the mean has shifted toward longer sternal lengths and larger chest sizes. In fact, whereas the eight traits associated with height and weight have moderate heritabilities (0.299-0.509), those associated with thoracic growth and development have heritabilities significantly lower (0.000-0.388), with ten out of twelve falling below 0.286.

Ahn (1990 and this volume) used a method of Lande and Arnold (1983) to measure selection from observed changes in phenotypic characters between two generations. After setting up genotypic and phenotypic correlation matrices of the twenty anthropometric traits previously mentioned, eight were chosen for further study. The remainder of the traits were eliminated because they were highly correlated with the first eight, since high correlations between traits may cancel or reduce the effect of selection on a particular trait. Ahn found that the standardized selection gradient for stature is negative and lower, while the standardized selection gradients for traits influencing thoracic volume are positive and higher. Since the directions of these selection gradients are those predicted by the observed size and morphology in this population and opposite in magnitude to the estimates of heritabilities of these traits, selection can be said to have occurred for smaller stature and larger chest sizes in this population.

Studies of Migratory Populations and Generational Change

Studies which document changes in body size and shape between sedentary and migratory populations can illuminate some of the characteristic changes which occur when groups move from one environment to another. When living conditions change, often changes in phenotypes accompany them. Boas (1912) documented changes in the bodily form of descendents of immigrants to the United States. He noted that in American descendents of

European heritage there were increased stature and slight but definite changes in head and face dimensions as well as the cephalic index. Boas ascribed these changes to influence of the environment. Rural-to-urban migration since the industrial revolution has been highly correlated with increases in stature and weight for offspring of migrant parents (Shapiro 1939, Goldstein 1943, Lasker 1946, Steegman 1985). Before the turn of the century, this change in phenotype was attributed to heterosis, or the increase in "genetic vitality" resulting from intermarriage between diverse groups, and the belief was that human types were fixed and would not change in response to the environment. Boas' landmark work pointed out that: 1) differences in parents and children were noticeable from birth and persisted into adulthood, 2) the longer the exposure to a new environment the more dramatic were the differences, 3) children from large families are smaller than those of smaller families even if they had the same "racial type", and 4) if parents of these children spent some of their own growth years in the new environment, parent-child differences were smaller (Bogin 1988). Boas' work established the nature of human developmental plasticity, and by extension, the concept of additive genetic variance in populations allowing for change in phenotypes under new environmental conditions.

While it is useful to compare sedentes resident at the migrants' destination with migrant offspring, migrant offspring can be compared with the sedentes in the environment of origin. Shapiro (1939) found the most similarity between recent Japanese immigrants to Hawaii and the villagers they left behind, and the most difference between these immigrants and Hawaii-born Japanese. The Hawaii-born Japanese were taller, and more linear in body build than either of the two other groups. Shapiro attributed the differences to the urban lifestyle and associated improvements in diet, medical care and socioeconomic conditions.

When rural-to-urban migration results in movement to slum-like urban environments, reductions in stature and weight can be seen, or there may be no difference between the migrant groups and those children left behind in impoverished areas (Malina et al. 1981, Bogin and MacVean 1981).

Several studies support the idea that migration behavior is selective, that is, that the migrant subpopulation may not be a random sample of the population (Shapiro 1939, Martin 1949, Kaplan 1954, Steegman, 1985). In general, migrants in these studies were taller and heavier than the populations either left or entered. Illsley et al. (1963) suggest that a correlation exists between physical type and socioeconomic status, such that only those who can afford to migrate and by association, those with superior nutrition, do so.

In conclusion, it appears that environment plays the primary role in determining short term changes which occur in growth and development in migrant populations. In contrast, it would be anticipated that changes which resulted from natural selection with consequent alteration of the genotype would not be easily reversible after one or a few generations, unless significant admixture takes place.

MATERIALS AND METHODS

The Study Populations

Puno, Peru is located in the altiplano, a high plateau of the central Andes. The Department of Puno borders the southwest edge of Lake Titicaca. The altitude, 3,900 m above sea level, and climate, present the inhabitants with extreme environmental stress. Although year-round temperatures do not vary much, diurnal variation in temperature is pronounced, with a daily high temperature of approximately 17 degrees Celsius, and below-freezing nightly temperatures. The adobe homes are not usually heated. The culture is predominantly agricultural, and diet consists of locally cultivated grains and tubers supplemented by meat and dairy products from local herds of llamas, alpacas, and sheep. Fish from the lake provide another protein source, but are not consistently available. Due to the unique climatological conditions, drought is a frequent occurrence. Poor soil, unpredictable rainfall, and isolation from outside sources of goods often result in a diet that is marginally adequate for residents of the altiplano. Hypoxia presents the most stressful environmental condition; at an altitude of 3,500 m oxygen pressure is reduced by about 35% compared to sea level.

Subjects from the high altitude environment, high altitude ancestry group were from Camacani, a village in the Department of Puno of about 2,100 individuals, located on the western shore of Lake Titicaca. All subjects (N=443) were born and raised in this high altitude environment, and were chiefly of Aymara descent. There were 184 females and 259 males. They ranged in age from several months through 19 years. This group was a subset of a sample of individuals of all ages in Camacani.

The city of Tacna, located in the fertile coastal area of southern Peru, is a processing and agricultural center with a population of approximately 100,000 individuals. Tacna is 35 km inland from the Pacific Ocean, and 380 km south of Camacani, with a consequent drop in altitude of 3,340 m between the two communities. The low altitude (560 m above sea level) and dry semitropical climate suit this area to production of sugar cane, cotton, wheat, fruit and alfalfa when rainfall is supplemented by irrigation from the Rio Caplina, a river drawing

204

water from the Andes. Cotton, sugar and fruit processing, and wine and liquor distilling, are main industries, and mining of copper, silver, borax, gypsum and sulphur is prevalent. Diet is more varied and food supplies are more adequate than in the altiplano. Meat is consumed regularly along with fruits and vegetables, and marketplaces provide sources for a variety of products from outside the immediate vicinity (Erickson et al. 1965). The population is therefore urbanized and has a good nutritional intake while not being subjected to the hypoxia and cold stress of the altiplano.

Low altitude subjects of high altitude ancestry from Tacna (N=218) ranged in age from 6 months through 19 years and were all born and raised at low altitude. There were 114 females and 104 males. They were the offspring of migrant parents who had been born and raised in the altiplano region of Puno, Peru. This group comprised both Aymara and Quechua speakers. Most data were collected from a population of school children in the large Catholic school of San Martin de Porres within the city of Tacna, but data from individuals below the age of six and above the age of 17 were also gathered in neighborhoods from which the school children came.

The Procedures of the Study

All subjects or their parents answered questionnaires regarding sex, age, date of birth, names and ages of family members, length of time of residence in the area, and languages spoken in the home. Subjects in Tacna also were asked about the length of time their parents had been resident in Tacna and the locations from which their parents had migrated. Subjects were questioned carefully to determine that they had been continuous lifelong residents of either the altiplano or low altitude environment. In Puno, individuals who had been lifelong residents were assumed to be offspring of other lifelong residents of the high altitude environment. In Tacna, only those individuals who were the offspring of migrant parents from altitudes above 3,500 m above sea level were included in the analysis. Subjects not fitting the model were eliminated from the study. Most birth dates were confirmed with the local Office of Civil Registration.

Anthropometric measurements were taken in 1978 and 1981 in Puno and Tacna, respectively, by the methods prescribed in the International Biological Programme handbook (Weiner and Lourie 1969). Twenty measurements were taken on each individual by several field workers trained in anthropometric procedures. Some of the same workers were present in both locations, providing intra-observer consistency. The skeletally-related traits measured were chosen to reflect thoracic growth and development on a background of overall stature and

nutritional status. The data, therefore, provide cross-sectional samples of individuals of different sexes in two environments from a few months of age to late adolescence or early adulthood. The two groups have in common parents of high altitude origins from the same region of southern Peru.

Overall body size is reflected in measurements of weight (WT), stature (HT) and sitting height (SH). Body composition or nutritional status can be portrayed by upper arm circumference (UAC) and skinfold measurements by skinfold calipers. Skinfold measurements collected for this study were subscapular skinfold (SS), suprailiac skinfold (SIS), midaxillary skinfold (MAS), and triceps skinfold (TS). Although thoracic dimensions are reflected in all the remaining twelve traits, some of these are also indicative of trunk size and overall body size, such as acromial height (AH), biacromial diameter (BD), bi-iliac diameter (BID), and sternal height (STH). Dimensions limited to a more specific picture of chest size and development include those which are linear, such as the antero-posterior depth of the thorax at the level of the union of the third and fourth sternabrae (APT), the antero-posterior depth of the chest at the level of the manubrium (APM), and the antero-posterior depth of the chest at the substernal level (APS). Transverse diameter of the thorax (TD) measures breadth at the level of the union of the third and fourth sternabrae. Volumetric measures of the thorax include chest circumferences taken at the level of the union of the third and fourth sternabrae during rest (TCN), during forced inspiration (TCFI) and forced expiration (TCFE), and chest circumference at the substernal level (SCN) during rest. Appendix A contains a list of the twenty traits in tabular form, and includes descriptions of the dimensions.

Statistical Analysis

Age was calculated for each individual by the method in Weiner and Lourie (1969), based on date of birth and date that measurements were taken. Data were sorted by location, that is, high or low altitude environment, and by sex. Individual values were grouped by year of age, for example, a female aged 3.98 years was placed in a group with other females 3.00-3.99 years of age. Plots were drawn to describe the progression in growth with age for each group and for each trait. Appendix B contains these plots, which compare the low altitude group and high altitude group by sex and trait.

Since one of the goals of this study was to determine whether actual differences are present between low and high altitude groups of high altitude ancestry, it was expected that growth curves would provide the necessary information. In fact, growth curves give no statistical information about those differences. This is because at points the curves cross and

recross, whereas at other points there may be marked differences between the groups. Plots may be valuable to determine how groups differ at *a specific age,* but as an objective measure of group differences they lack utility. Another method was derived therefore to quantify differences between groups and determine with what degree of certainty they might actually be different.

A regression was therefore performed separately for each trait by sex according to a method for regression analysis using a qualitative variable described by Neter et al. (1985). The model, where X_{i1} = the decimal age for individual i, Y_i = the response (that is, the specified trait value for individual i), and E_i = the error term, also includes a qualitative variable X_{i2}, which = 0 if the individual i is a Tacna subject or = 1 if the individual i is a Puno subject. The model is, therefore:

$$Y_i = B_0 + B_1 X_{i1} + B_2 X_{i2} + E_i,$$

and the response function for this model is:

$$E(Y) = B_0 + B_1 X_1 + B_2 X_2 .$$

To understand the regression parameters, consider the case where the trait is from the low altitude group (X_{i2} = 0). We have as the response function:

$$E(Y) = B_0 + B_1 X_1 .$$

Coefficient B_0 is the intercept for the response function of the low altitude group. Coefficient B_1 indicates the slope of the response function for the group.

Consider, then, the case for a trait from the high altitude group (X_{i2} = 1). The response function becomes:

$$E(Y) = B_0 + B_2 + B_1 X_1.$$

The sum of coefficients B_0 and B_2 indicate the intercept for this response function, while the slope B_1 is the same as the slope for the response function for the low altitude group. Coefficient B_2, therefore, indicates the average difference between the two groups.

A 95% confidence interval can be calculated for the coefficient B_2 by computing B_2 plus or minus the standard error for the B_2 multiplied by the t-value based on the number of degrees of freedom for error for that particular regression. If the computed confidence interval contains the value zero, this indicates that there is the possibility that there is no true difference between the two groups. If the confidence interval does not contain the value zero, then the groups are indeed different, and it is noted, that with 95% confidence, the true average difference between the groups falls somewhere within that confidence interval. P-values, which indicate the probability that the differences of this magnitude will be observed given that the true population difference is equal to zero, are generated during the regression analysis as well. The analyses were carried out with SAS statistical programs.

For each of the twenty anthropometric traits, therefore, mean differences between the high altitude and low altitude groups were calculated, with confidence intervals providing a formal test of whether $B_2 = 0$. P-values as well as confidence intervals are reported in the next chapter.

RESULTS

Discussion of Sample Sizes

The data on the Tacna and Puno children and adolescents are cross-sectional and therefore represent information unique to each population for the particular time in which it was gathered. All measurements were made in a period of several weeks. Cross-sectional studies, while not as comprehensively informative as longitudinal studies which follow a particular group over time, are a useful compromise because they are less expensive and time-consuming to carry out and allow for more flexibility in personnel who do not need to remain available for a longitudinal study. Both data sets contain measurements from children in the same families and single children. The number of individuals represented by the data is comparable to that used in other similar studies of growth and development in Peruvian populations (Frisancho and Baker 1970, Frisancho et al. 1975, Beall et al. 1977, Boyce et al. 1974).

Sample sizes for particular age groups are small. These are shown in Table 1. This fact caused difficulty in analyzing the data in any way which required separating them according to age group, such as within plots. Sample size must be sufficient to reduce the standard error and therefore increase the level of confidence in the precision of results (Goldstein 1986).

Henceforth, comments about the plots (Appendix B) will be restricted to characteristics of the curves for those ages between the age groups six and sixteen, because sample sizes for those

Table 1. Age Distribution for Tacna and Puno Samples

Age Group	Age (years)	Puno		Tacna	
		Males	Females	Males	Females
1	0.00-1.39	10	7	0	1
2	1.40-2.69	11	12	0	1
3	2.70-3.99	8	10	2	1
4	4.00-4.99	8	10	1	2
5	5.00-5.99	7	8	3	0
6	6.00-6.99	8	9	7	5
7	7.00-7.99	12	13	2	6
8	8.00-8.99	9	12	8	7
9	9.00-9.99	15	9	10	5
10	10.00-10.99	19	11	11	7
11	11.00-11.99	15	5	7	8
12	12.00-12.99	12	8	7	11
13	13.00-13.99	24	19	13	21
14	14.00-14.99	17	13	15	17
15	15.00-15.99	30	14	7	13
16	16.00-16.99	17	7	6	7
17	17.00-17.99	15	8	3	0
18	18.00-18.99	13	7	1	2
19	19.00-19.99	9	2	1	0
Totals		259	184	104	114

below age six and above age sixteen were especially small for the Tacna group. The regression analyses performed on the data included data from all age groups, as similar analyses done on age groups six through sixteen exclusively were not significantly different.

<u>Plots</u>

The growth patterns of the high altitude population of Puno with respect to these twenty anthropometric traits have been described previously by Ahn (1990). In general, sexual dimorphism is apparent for stature and weight at 15 to 16 years of age. Stature increases until age 18 for females and 22 for males. Weight increases for males until about age 22 and for females until age 17. Sternal length increases until age 18 for males and 14 for females, and at age 14 sexual dimorphism for this trait is evident. For both males and females, skinfold measurements increase slightly from about age 3 to about age 9, with females surpassing males at all ages. Sexual dimorphism for skinfold measurements is apparent at about age 10. Females have increased amounts of body fat into adulthood.

Chest dimensions exhibit differences between the sexes as well. In general, late sexual dimorphism is the rule, with definitive differences appearing in the third decade. Thoracic circumference continues to increase until age 22 for males and age 20 for females. Overall, patterns of age change in the Puno sample show that this population has greater chest circumferences than low altitude populations, and therefore has accelerated growth in thoracic size relative to stature.

There is no discernible adolescent growth spurt for either males or females from Puno with respect to either weight or linear dimensions of stature. For males, skinfolds increase more rapidly in size after the age of 9, relative to earlier ages, which may signal hormonal processes related to puberty. Females experience significant rapid increases in skinfolds after age 9 which may also be related to pubertal changes.

Because of the limited amount of data available for the Tacna group at low and high ages, it is not readily apparent for all traits what the patterns for cessation of growth and sexual dimorphism are. In general, where sexual dimorphism is evident, the Tacna group displays it much earlier than the Puno group. For weight, Tacna individuals show no sexual dimorphism, but since females have increased amounts of body fat relative to males, and males are taller, this lack of difference at higher ages probably reflects a trade-off between increased weight due to greater stature for males and increased body fat for females. A growth spurt is slightly apparent at ages 11-13 for weight in the Tacna group. For stature, a growth spurt is not evident in the Tacna group. Sexual dimorphism is present in stature as early as age 13, and males from both Tacna and Puno exceed females overall above the age of 15. As might be expected from the presence of sexual dimorphism in stature, sexual dimorphism is also present in sitting height, with differences apparent about age 15.

Body composition presents more variability within both groups. Undoubtedly, endocrine processes are playing roles in pubertal changes which in turn are enmeshed with nutritional factors. Upper arm circumference in the Tacna group increases for both sexes at a steadier rate over all age groups than within the Puno group, which has more noticeable increases at puberty. Subscapular and suprailiac skinfolds are greater and display greater increases over time in Tacna females than Tacna males. Triceps skinfolds are greater in Tacna females than males, but females from both locations exceed males overall after age 10. Midaxillary skinfolds are the most variable trait of all, with high standard errors for both groups at all ages. Tacna males and females both have large midaxillary skinfolds compared to Puno males, but Puno females have extremely larges measures for this trait after the age of 10.

The plots for growth in thoracic traits do not reveal any growth spurts within groups of Tacna individuals, with the exception of sternal height. Although there is no sexual dimorphism for this trait at the ages available, a growth spurt occurs for females around the ages of 9 to 13 and for males slightly later, at about 10 to 14 years of age. This is a linear measure related to stature in addition to thoracic size and development. Sexual dimorphism is evident in a number of other traits, including biacromial diameter, bi-iliac diameter (evident at age 10), and all measures of thoracic circumference (evident at age 15). This is in contrast with sexual dimorphism for the Puno group, which is manifested as late as the third decade. It is possible, however, that more data at later ages for the Tacna group might alter this picture if available, but early dimorphism seems clear from this data set. Acromial height for all groups is strikingly similar at age 16, whereas for height at age 16 males from both groups exceed females, indicating that males have longer lower limb length at this age, and overall, trunk length is about the same for all sexes and locations.

The information from plots must be viewed with caution, as noted before, because of small numbers of individuals in each age group. Plots are most useful to examine effects of environment and sex at specific ages but do not give estimates of whether populations as wholes are actually different from each other. The next section will describe the results of regression analyses performed on trait values which quantify differences between the populations from Puno and Tacna.

Regression Analysis

Results for each trait by sex and by age are given in Table 2 through Table 5. Tables 2 and 3, which show results for traits which primarily reflect overall body size and composition,

are for females and males, respectively. Tables 4 and 5, which provide results for those traits which reflect trunk size and thoracic size and development, are for females and males, respectively. Each trait is listed, and beside it is the location of the group for which that trait value mean is greatest, followed by the 95% confidence interval indicating the range within which the true mean difference would be found. The P-value of the analysis is then given. Traits for which there were no significant differences between the low and high altitude groups are listed last in each table. As noted previously, these results were derived from a regression technique which uses the total sample to determine which population possesses greater mean values where simple plots cannot give that information.

Table 2 reports the results for low and high altitude comparisons of females with respect to overall body size and composition. For all traits except midaxillary skinfold and triceps skinfold, Tacna females are larger than Puno females, with highly significant p-values.

Table 2. Females: Traits Reflecting Overall Body Size and Composition

Trait	Highest Mean	95% C.I. for Mean Difference	P-value
Weight	Tacna	2.52-5.66 kg.	$p<0.0001$
Stature	Tacna	3.19-6.37 cm.	$p<0.0001$
Sitting height	Tacna	2.67-4.41 cm.	$p<0.0001$
Midaxillary skinfold	Puno	1.04-2.34 mm.	$p<0.0001$
Subscapular skinfold	Tacna	3.23-6.13 mm.	$p<0.0001$
Suprailiac skinfold	Tacna	1.65-4.10 mm.	$p<0.0001$
Upper-arm circumference	Tacna	1.48-2.50 cm.	$p<0.0001$
Triceps skinfold			

Table 3. Males: Traits Reflecting Overall Body Size and Composition

Trait	Highest Mean	95% C. I. for Mean Difference	P-value
Weight	Tacna	3.42-5.95 kg.	$p<0.0001$
Stature	Tacna	5.56-8.61 cm.	$p<0.0001$
Sitting height	Tacna	2.43-4.30 cm.	$p<0.0001$
Midaxillary skinfold	Tacna	0.57-1.51 mm.	$p<0.0001$
Subscapular skinfold	Tacna	1.01-2.30 mm.	$p<0.0001$
Upper-arm circumference	Tacna	1.46-2.94 cm.	$p<0.0001$
Triceps skinfold	Tacna	0.61-1.84 mm.	$p<0.0134$
Suprailiac skinfold			

Although skinfold measures are higher overall in the Tacna group, mean differences never exceed 0.6 cm, whereas differences in stature and weight are high. The mean difference for stature falls within the range of 3 to 6 cm. and the mean difference for weight is between 2.5 and 5.7 kg. Differences in body fat appear to be relatively small, therefore, and large differences between these two populations may be more attributable to bone size and length and muscle distribution. There is no difference between the two groups for triceps skinfolds. Upper arm circumference is significantly higher in the Tacna group, indicating better overall nutrition for this group. Large midaxillary skinfold measures in the Puno group are characteristic for these females.

The comparisons for males with respect to body size and composition are shown in Table 3. Males from Tacna are taller, heavier and have greater amounts of body fat than Puno males, with the exception of suprailiac skinfolds. Mean skinfold differences are extremely small,

however, with no differences exceeding 2.3 mm. Suprailiac skinfolds are not significantly different. Upper arm circumference is higher in the Tacna group as well, with the mean difference somewhere between 1 and 3 cm. Again, this group is presumed to have superior nutrition, but fat deposition, while measurably different, is not extremely dissimilar, indicating that linear growth is accounting for the major differences seen in weight. The Tacna group is between 3.4 and 6 kg heavier, on average, and from 5 to 8 cm taller.

Table 4. Females: Traits Reflecting Thoracic Growth and Development

Trait	Highest Mean	95% C. I. for Mean Difference	P-value
Acromial height	Tacna	0.91-2.31 cm.	$p<0.0001$
Biacromial diameter	Tacna	1.34-2.32 cm.	$p<0.0001$
Bi-iliac diameter	Tacna	1.78-2.84 cm.	$p<0.0001$
Sternal length	Tacna	0.65-1.54 cm.	$p<0.0001$
Transverse diameter	Tacna	0.18-1.02 cm.	$p<0.0048$
Chest circumference	Puno	0.40-3.14 cm.	$p<0.0113$
Chest circumference, forced expir.	Puno	0.39-3.35 cm.	$p<0.0137$
Chest circumference, forced inspiration			
Chest circumference, substernal			
A-P diameter, manubrium			
A-P diameter, chest			
A-P diameter, substernal			

Table 4 presents results for female groups for traits related to thoracic growth and development. Tacna females have larger trunks, as indicated by larger measures of acromial height, biacromial diameter, and bi-iliac diameter. Transverse diameter was greater in this group, as was sternal length. P-values were highly significant for all of these traits. Puno subjects had larger chest circumferences for both resting and forced expiration measures.

Table 5. Males: Traits Reflecting Thoracic Growth and Development

Trait	Highest Mean	95% C.I. for Mean Difference	P-value
Acromial height	Tacna	1.49-1.62 cm.	$p<0.0001$
Biacromial diameter	Tacna	1.55-2.52 cm.	$p<0.0001$
Bi-iliac diameter	Tacna	0.50-1.17 cm.	$p<0.0001$
Sternal length	Tacna	0.61-1.38 cm.	$p<0.0001$
A-P diameter, chest	Puno	0.22-0.78 cm.	$p<0.0005$
A-P diameter, substernal	Puno	0.15-0.72 cm.	$p<0.0027$
Chest circumference	Tacna	1.95-4.02 cm.	$p<0.0001$
Chest circum., forced inspir.	Tacna	3.43-5.43 cm.	$p<0.0001$
Chest circum., forced expir.	Tacna	2.51-4.44 cm.	$p<0.0001$
Chestcircum., substernal	Tacna	0.86-2.55 cm.	$p<0.0001$
Transverse chest			
A-P diameter, manubrium			

P-values for these two tests were less significant. For all the remaining traits, there were no significant differences. Chest circumferences, both during forced inspiration and at the substernal level, showed no differences. All three measurements of antero-posterior thoracic dimensions were equivalent when regressed on age and compared to each other.

The male groups are compared for thoracic measures of size and shape in Table 5. Again, Tacna subjects have larger linear trunk size, as indicated by comparisons of acromial height, biacromial diameter, and bi-iliac diameter. This coincides with larger stature measures previously seen. Sternal length is greater in the Tacna group, and the 0.61-1.38 cm confidence interval is similar to that of 0.65-1.54 cm range seen for females. Puno subjects have larger antero-posterior measures at the level of the third and fourth sternabrae, and substernally. Tacna males are larger for all four measures of chest circumference. The range of differences between chest circumferences is from somewhere between 0.86-2.55 cm for substernal circumference to somewhere between 3.43-5.43 cm for circumference during forced inspiration. All differences between groups are highly significant. There are no differences between the groups for transverse chest measures and measures of the antero-posterior diameter at the level of the manubrium.

To summarize, therefore, both males and females from Tacna are larger and heavier than their Puno cohorts, with major differences being represented by stature, and weight related to that increased stature, but not body fat. Tacna females are at least as big for five traits representing thoracic growth, and bigger for five more, whereas Puno females exceed Tacna females for two of these twelve traits. Tacna males are at least as large as Puno males for two of twelve traits related to thoracic size and larger than Puno males for eight more. Puno males are larger than Tacna males with respect to two antero-posterior measures of the thorax.

DISCUSSION AND CONCLUSIONS

Overview of Results

Could natural selection have acted upon high altitude populations, giving them the unique skeletal characteristics seen today? The altiplano has been inhabited for at least 10,000 years, or 500 generations, and possibly longer, enough time for isolated groups such as the Aymara and Quechua to develop adaptations to hypoxia. The unusual traits of these people are highlighted by the fact that mountain inhabitants around the world do not show the large chests typical in the Andes. Beall (1980) reports that Andeans have the highest values of chest circumference relative to stature of any high altitude population studied. Sherpas from

the Himalayas and Ethiopians have probably been resident at high altitude for shorter periods of time, have more low altitude admixture, and more seasonal migratory behavior than Andean people, who are isolated by distance and surrounding mountains and have developed self-sufficiency in the altiplano environment year round.

Comparison of two groups of children of high altitude ancestry has shown that these groups are both similar and different. While the low altitude group is taller and heavier, differences are mostly attributable to stature, not fat distribution. Although data are sparse for the upper age groups, the terminal point of growth may be similar for females, indicating that differences are most apparent during the growth period. Male growth for Puno does not cease until approximately age 22, and the Tacna sample has no subjects over 19, but it is possible that the adult stature for both is similar. Frisancho and Baker (1970) found that adult stature was similar for Nuñoa males, sea-level Peruvians, and U. S. males when corrected for weight. Both the Puno and Tacna samples lack adolescent growth spurts, another similarity. Most significantly, the chest dimensions for Tacna males and females were overall at least as great or greater than those of Puno males and females. Sternal length, one of the most noticeable traits of highlanders in the Andes, is significantly increased in Tacna children. If hypoxia were responsible for short term developmental increase in chest sizes, the Tacna group would be expected to show a loss of chest size after just one generation away from hypoxic stress. In fact, the chest sizes of Tacna males are absolutely greater than or equal to those of Puno males. For females, the picture is less conclusive, but for most of the traits, Tacna females have thoraxes at least as large as those of the Puno females, and exceed them for transverse diameter and sternal length in addition to three other traits. The Tacna population has been sampled at an opportune time to compare body shapes before another generation is born, with almost certain lowland admixture.

Reliability of Results

As with all data sets and analyses, there are shortcomings for this one. In addition to the need for additional subjects at particular ages, it would have been advisable to have a low altitude group of low altitude ancestry as a control group. In reality, this is difficult to accomplish because of the large degree of admixture which has occurred in coastal populations in the last century from other South American groups, Europeans, and Africans. Additionally, any low altitude group could contain a high proportion of genes from high altitude populations. When comparing the Puno sample to that of Nuñoa (Baker 1969, Frisancho and Baker 1970), however, they are similar in growth data for those traits which are documented. This

similarity provides a starting point for further comparisons. Future data collection should include a control population if possible.

The argument can be made that significant differences in chest sizes between the groups could be due to overlying fat and muscle. At points where skinfold measures are the same at specific ages, however, the chest measures remain greater, indicating that chest sizes for the Tacna group are absolutely larger in those cases. Results for the female groups are not as clear as for the males. Breast development may confound measurements in subjects after puberty, accounting for the extremely variable measures of skinfolds in females. It is notable that many studies of high altitude Peruvian children and adolescents have been done on males only.

The Tacna group contains both Quechua and Aymara speaking subjects, whereas the Puno sample is exclusively Aymara. This blend of ethnic backgrounds will complicate the data from a genetic standpoint. Both peoples have been long term residents of the altiplano, however, and studies suggest that both have experienced natural selection as a result (Boyce et al. 1974, Arnaud et al. 1985).

Selective migration may have occurred in the Tacna parents, such that those who were originally larger and taller as a result of better family economic conditions came to the coast from the altiplano. If this has happened, the results could have been skewed. Comparisons of these parents could be made to adults remaining in Puno. Since the parents of Tacna children include matings made before and after migration, however, the degree of endogamous and exogamous matings (relative to the communities of origin) will affect the variance seen in trait measurements. While comparisons between the parental group of Camacani, a small village with a presumably high inbreeding coefficient, and the parental group of the Tacna children, drawn from the entire Puno region, are possible, they would not necessarily be meaningful.

Other Factors

The Tacna subjects do not experience the degree of environmental stress that the Puno subjects do: the climate is more temperate and hospitable to human life, there is no hypoxia, and the urban environment gives access to foods and services not available in the altiplano. What are the greatest environmental influences on growth and development? Cultural practices which differ between the groups will also affect body size and shape. The altiplano natives have a greater level of physical activity necessitated by their subsistence agricultural lifestyle. While undernutrition might be present, Picón-Reátegui (1976) concluded that the dietary intakes in Nuñoa meet U. S. dietary recommended allowances. In fact, Leonard and Thomas (1989) found that children of the altiplano experience little seasonal variation in food

intake and concluded that they are more buffered than adults during preharvest times when food supplies are lowest. Camacani dietary intakes may actually exceed those of Nuñoa, since Lake Titicaca provides sources of protein not available in Nuñoa. This study supports the idea that Tacna and Puno children are not grossly different in skinfold measures, and by extension, fat deposition. Females in Puno marry and bear children at a younger age than do Tacna females, who have assumed a more urban, modern approach to marriage and childbearing. The fat deposition for the Puno females may be culturally determined, as they prepare for relatively early reproductive functions by increasing energy resources. Female growth is closer to the well-nourished standard than male growth, possible a selective advantage conferred to assure reproductive success (Stini 1971). Environmental and cultural factors therefore interact to affect body size and shape.

McFarlane (1990) reports that growth in highland children may be affected by the presence of cryptic or overt infections. In a study of Chilean highland children, 40% were found to harbor infections of the respiratory or sensory systems, skin, or gastrointestinal tract. This rate of infection was 50% higher than that seen in coastal dwelling children of Spanish descent. Weight gain differentials were significant between well and infected highland children and mothers of infected children reported unsatisfactory weight gains. Differences in health could also result in different growth curves for the Puno and Tacna samples.

Conclusions

Previous studies have supported environmental causation, whether developmental or genetic, for the characteristic skeletal morphology of Andean Quechuas and Aymaras. While some groups prefer the explanation that the large chests and small stature typical of Andean populations have their origin in a novel response with each new generation, others prefer to cite evolutionary forces, that is, natural selection, as the mechanism at work. Palomino et al. (1979), in a study of high altitude Chileans, feels that body size and body shape are under differing sources of control: 1) stature is under environmental control during the growth period, 2) the terminal point of growth, that is, final adult height, is more genetically determined, and 3) body shape is mostly genetically determined. Estimates of heritability of twenty anthropometric traits in Camacani subjects (Kramer 1980, Vandemark 1985, Ahn 1986; all in this volume), suggest that thoracic traits are under different genetic control than other traits for body size. Thoracic traits show lower heritabilities, suggesting that the additive genetic variance has been reduced as selection shifted the mean towards larger chest sizes. Ahn (1990 and this volume) showed that selection has operated more strongly on the thorax than on body

size, but directional selection has occurred to increase the chest dimensions and decrease stature.

When comparing two populations of high-altitude ancestry from different environments significant differences in size and thoracic dimensions are seen. Reduced environmental stresses in the low-altitude population have resulted in this group having greater body size during the growth period. In addition, the large thoracic dimensions seen in the low altitude population, in the absence of the hypoxia theorized to be important in development of similar dimensions seen in high-altitude populations, provide independent confirmatory evidence for a genetic component in the growth patterns of these Andean people.

Appendix A

ANTHROPOMETRIC TRAITS

AH	acromial height (from sitting surface to top of shoulders)
APM	antero-posterior diameter of chest (level of manubrium)
APS	antero-posterior diameter of chest (substernal level)
APT	antero-posterior diameter of chest (level at union of third and fourth sternabrae)
BD	biacromial diameter (breadth of shoulders)
BID	bi-iliac diameter (breadth of hips)
HT	stature
MAS	midaxillary skinfold
SCN	chest circumference (substernal)
SIS	suprailiac skinfold (above iliac crest)
SH	sitting height (from sitting surface to top of head)
SS	subscapular skinfold
STH	sternal length (from notch in manubrium to distal end)
TCFE	chest circumference (forced expiration)
TCFI	chest circumference (forced inspiration)
TCN	chest circumference (level at union of third and fourth sternabrae)
TD	transverse diameter of chest (breadth at level of union of third and fourth sternabrae)
TS	triceps skinfold
UAC	upper arm circumference
WT	weight

Appendix B

PATTERNS OF AGE CHANGE

The following pages will show the age distributions for twenty anthropometric traits. Plots are for males or females, and compare patterns of age change in the high altitude subjects and low altitude subjects.

ACROMIAL HEIGHT

FEMALES

□   Females — Tacna   +   Females — Puno
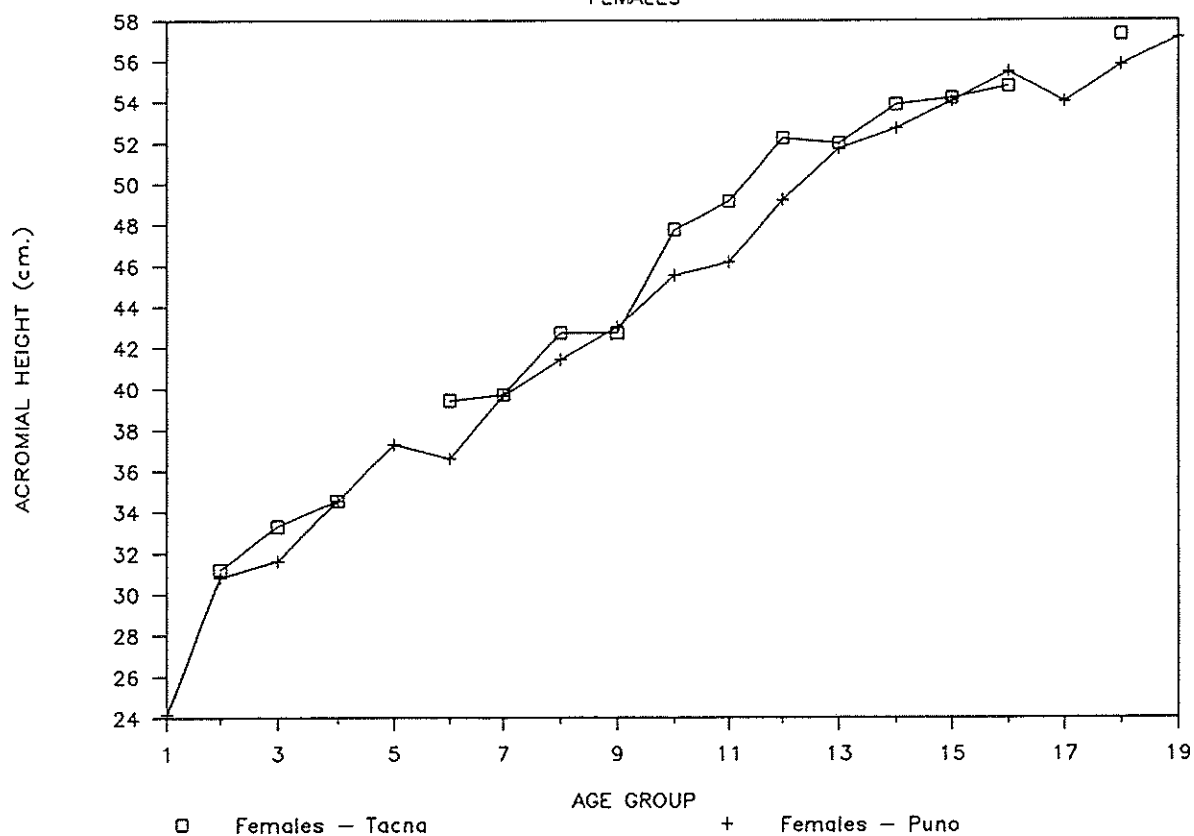
ACROMIAL HEIGHT

MALES

□   Males — Tacna   +   Males — Puno
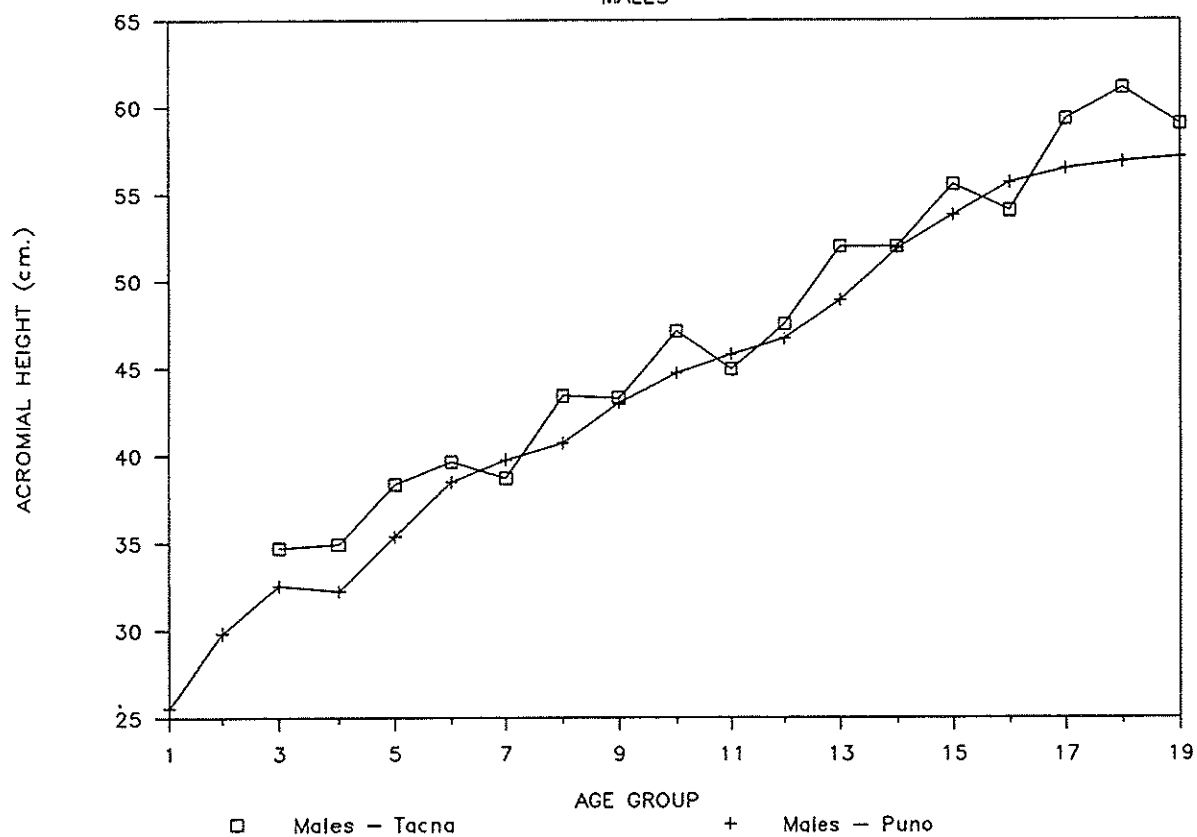
A–P DIAMETER, MANUBRIUM

FEMALES

□   Females – Tacna   +   Females – Puno
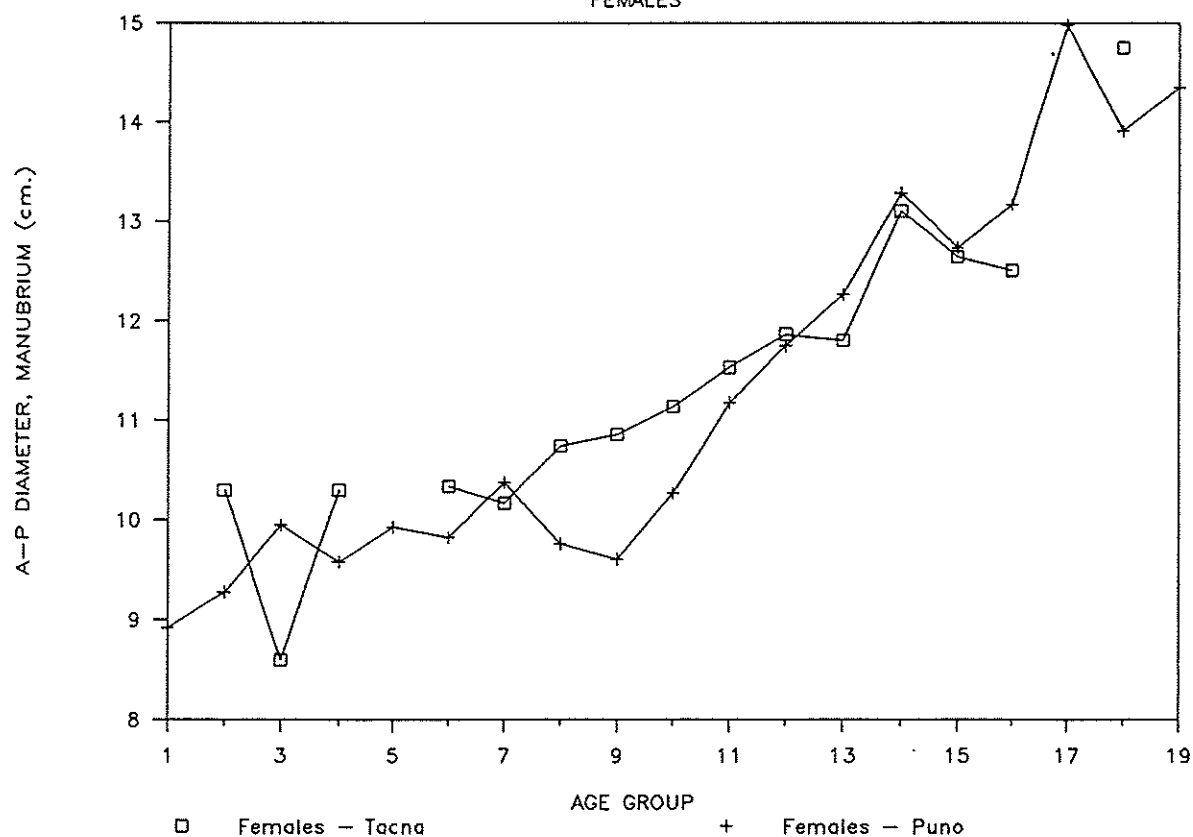
A–P DIAMETER, MANUBRIUM

MALES

□   Males – Tacna   +   Males – Puno
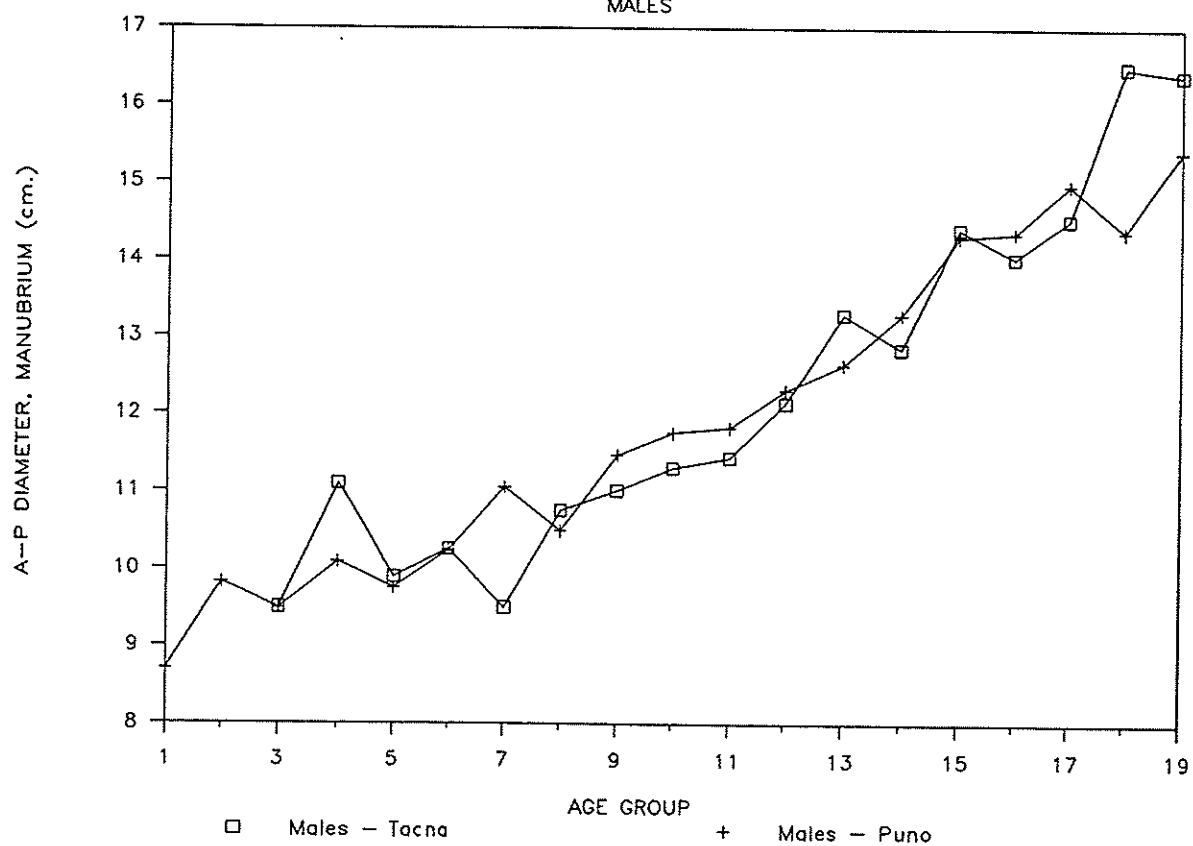
A-P DIAMETER, SUBSTERNAL
FEMALES
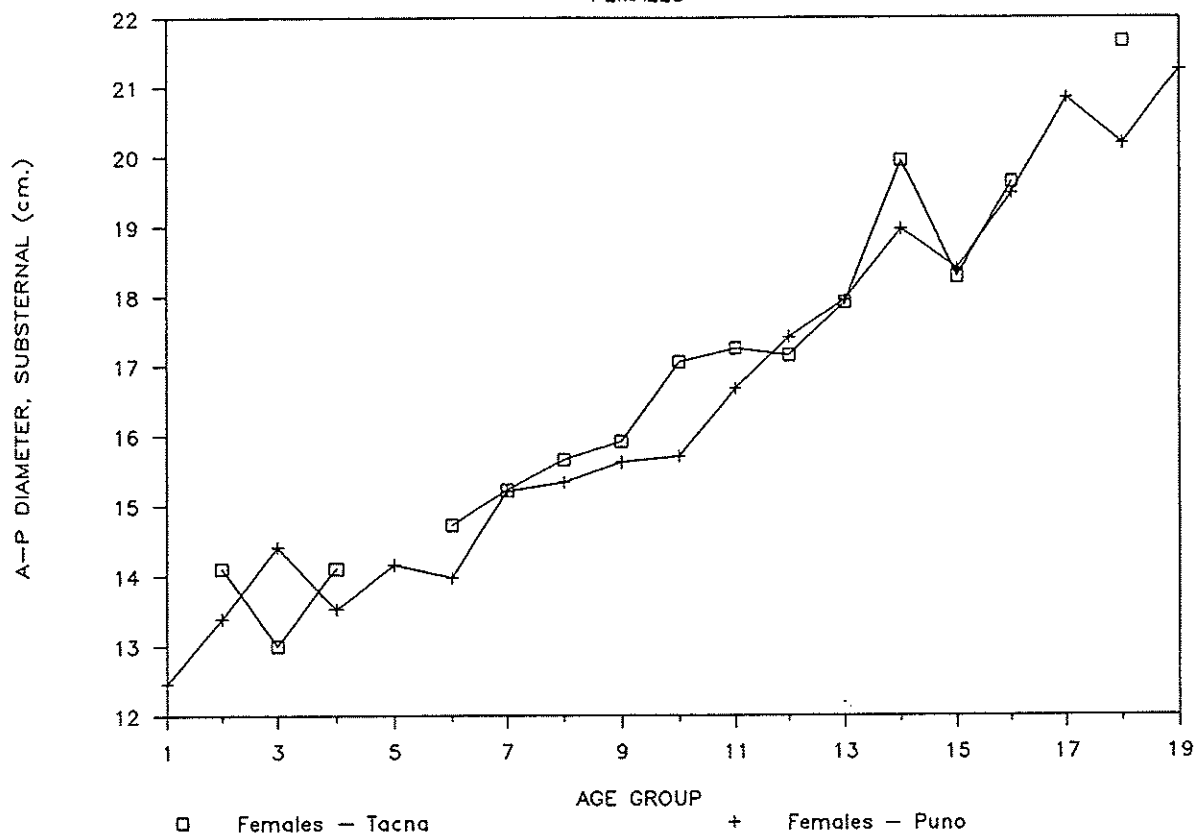
A-P DIAMETER, SUBSTERNAL
MALES
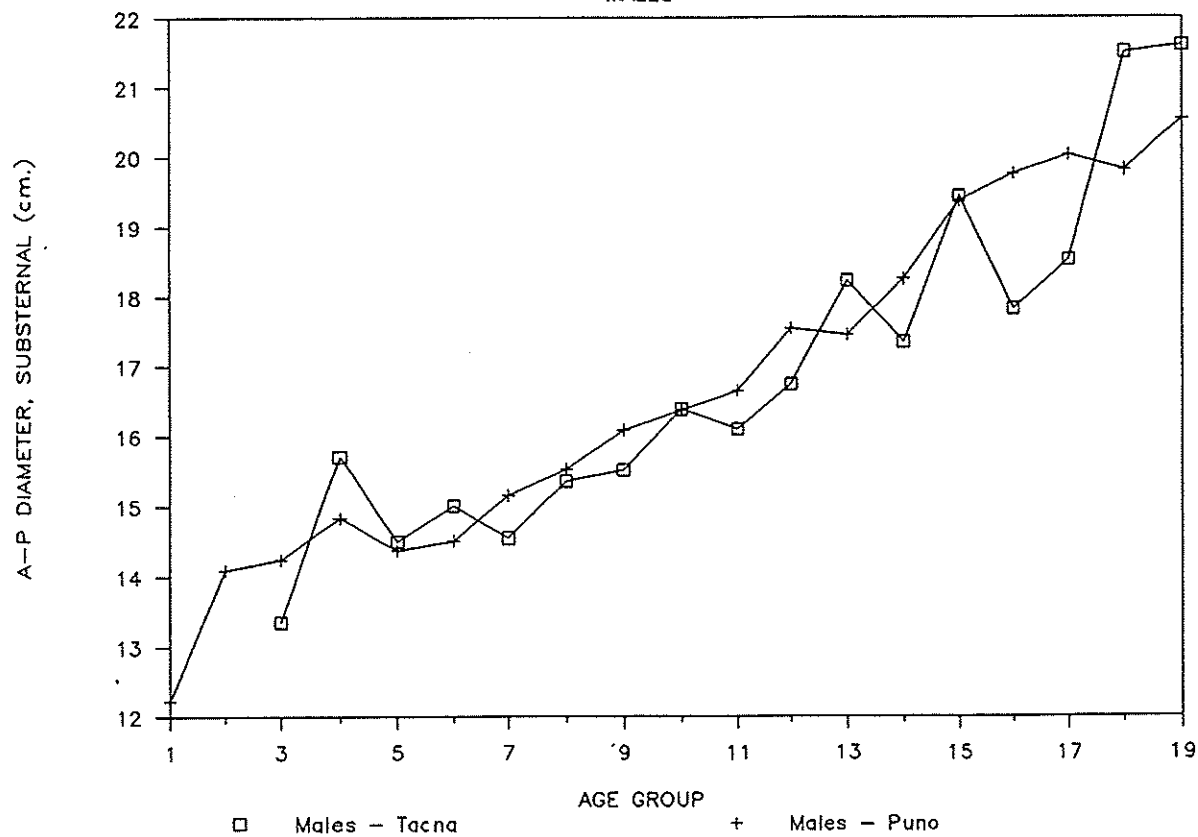
A-P DIAMETER, CHEST

FEMALES
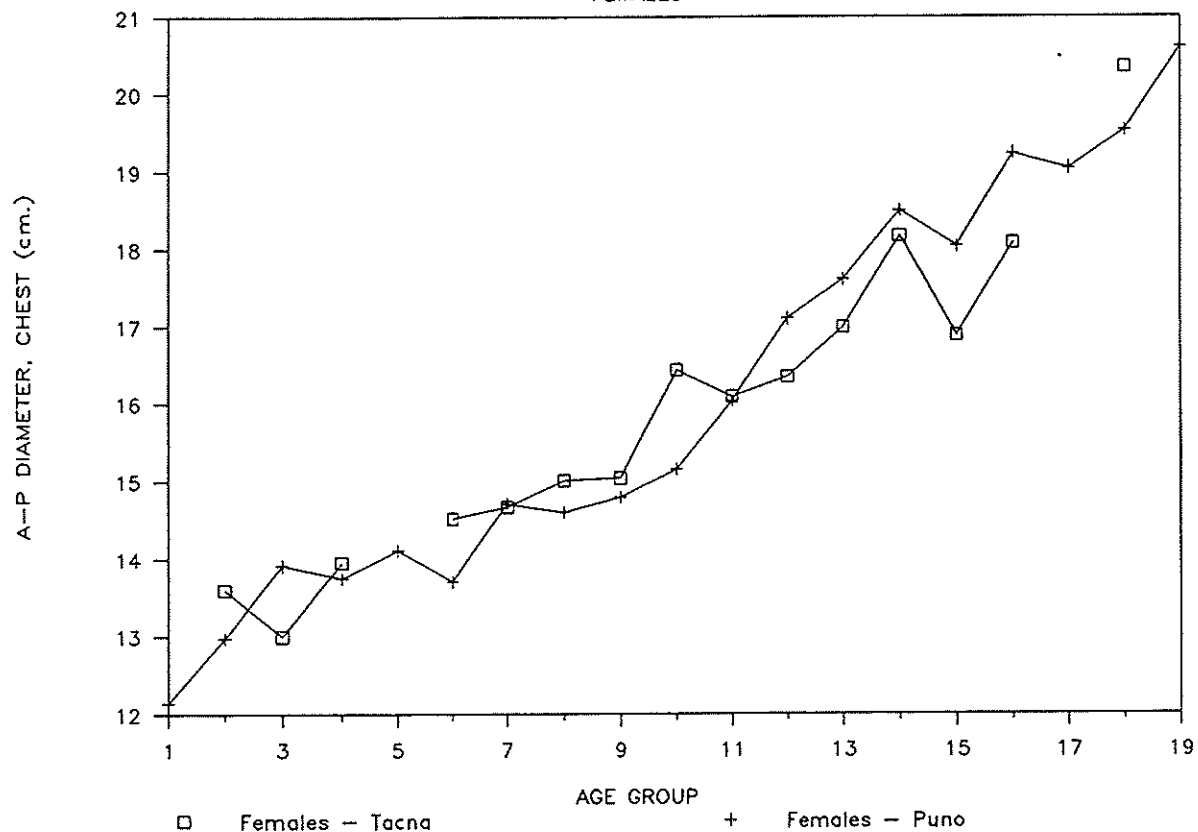
A-P DIAMETER, CHEST

MALES
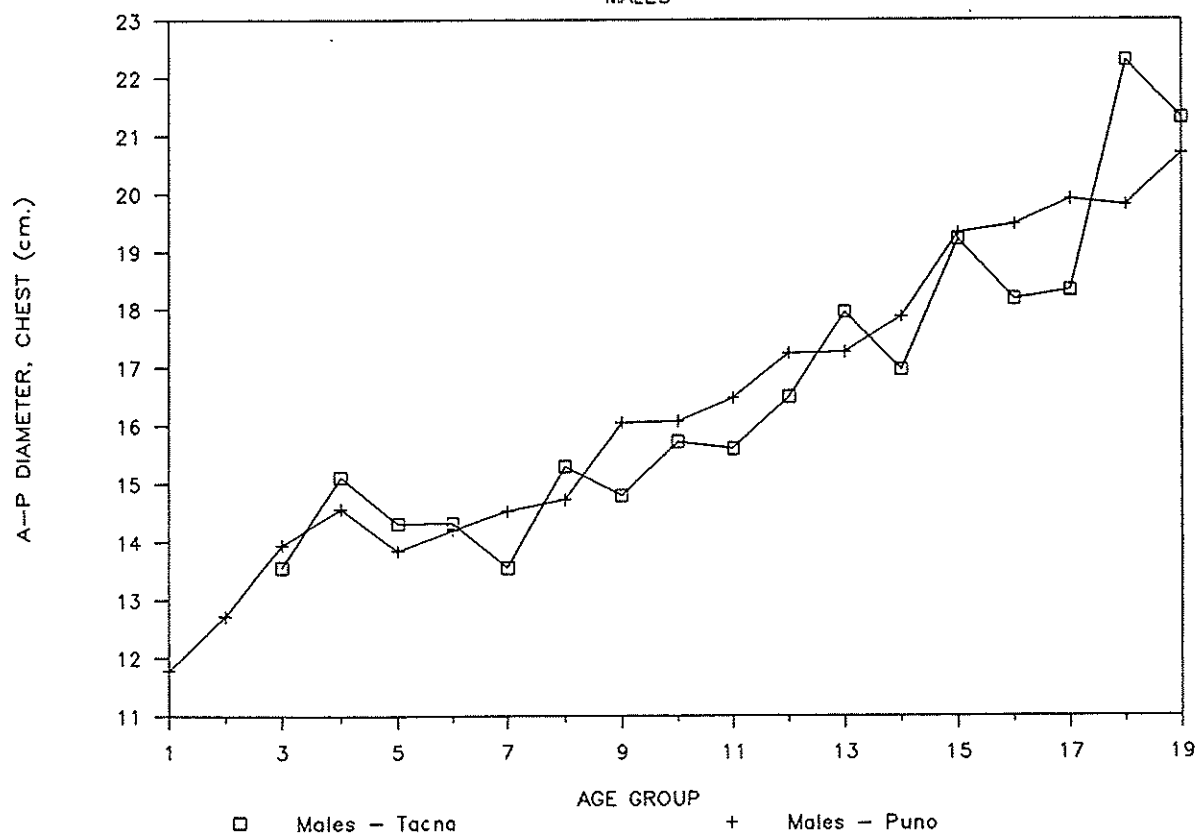
BIACROMIAL DIAMETER
FEMALES
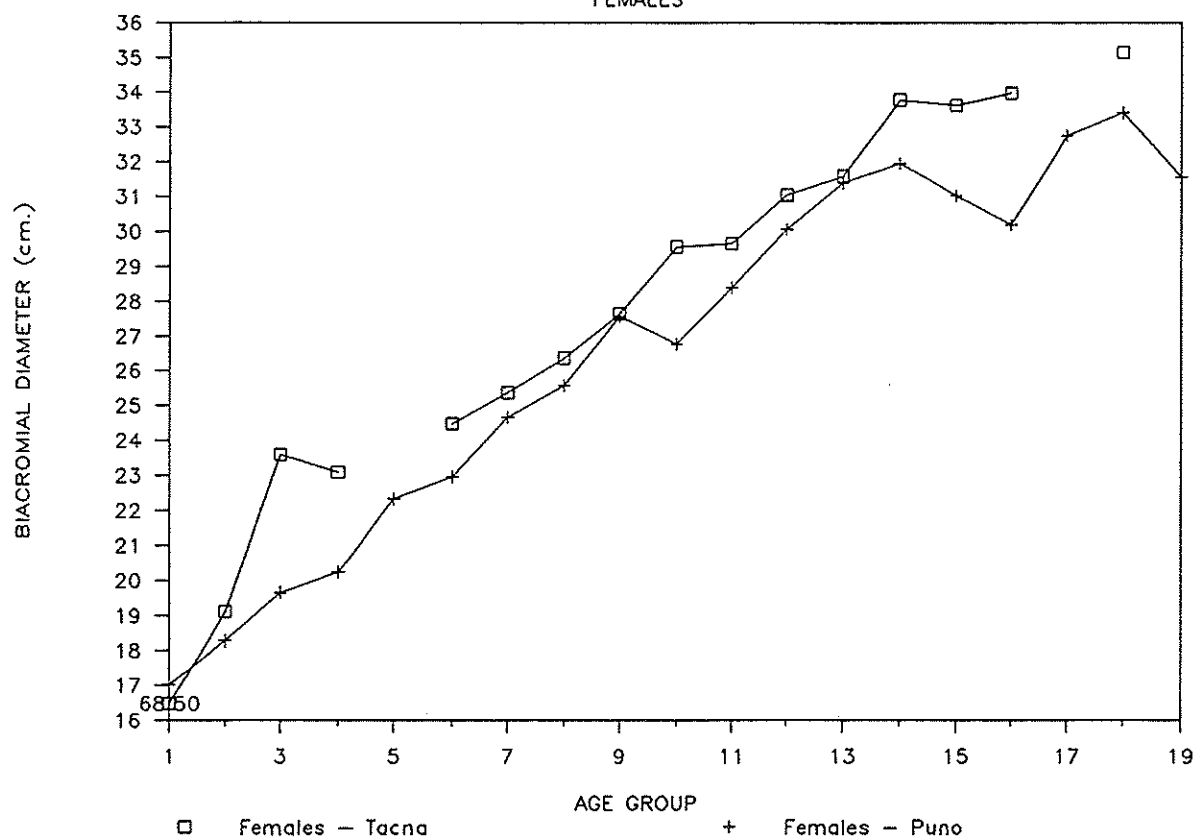
BIACROMIAL DIAMETER
MALES
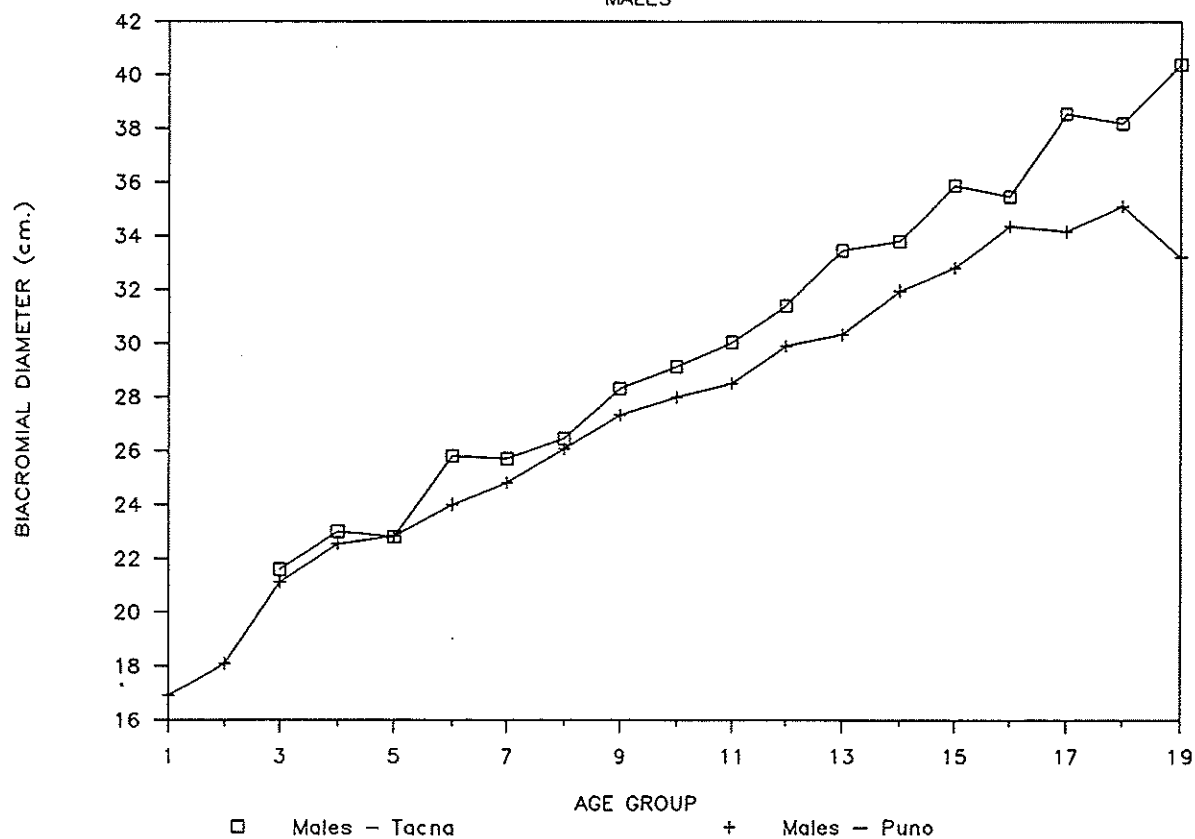
BI–ILIAC DIAMETER

FEMALES

Females — Tacna   +   Females — Puno

BI–ILIAC DIAMETER

MALES

Males — Tacna   +   Males — Puno

STATURE
FEMALES

Females — Tacna   + Females — Puno

STATURE
MALES

Males — Tacna   + Males — Puno
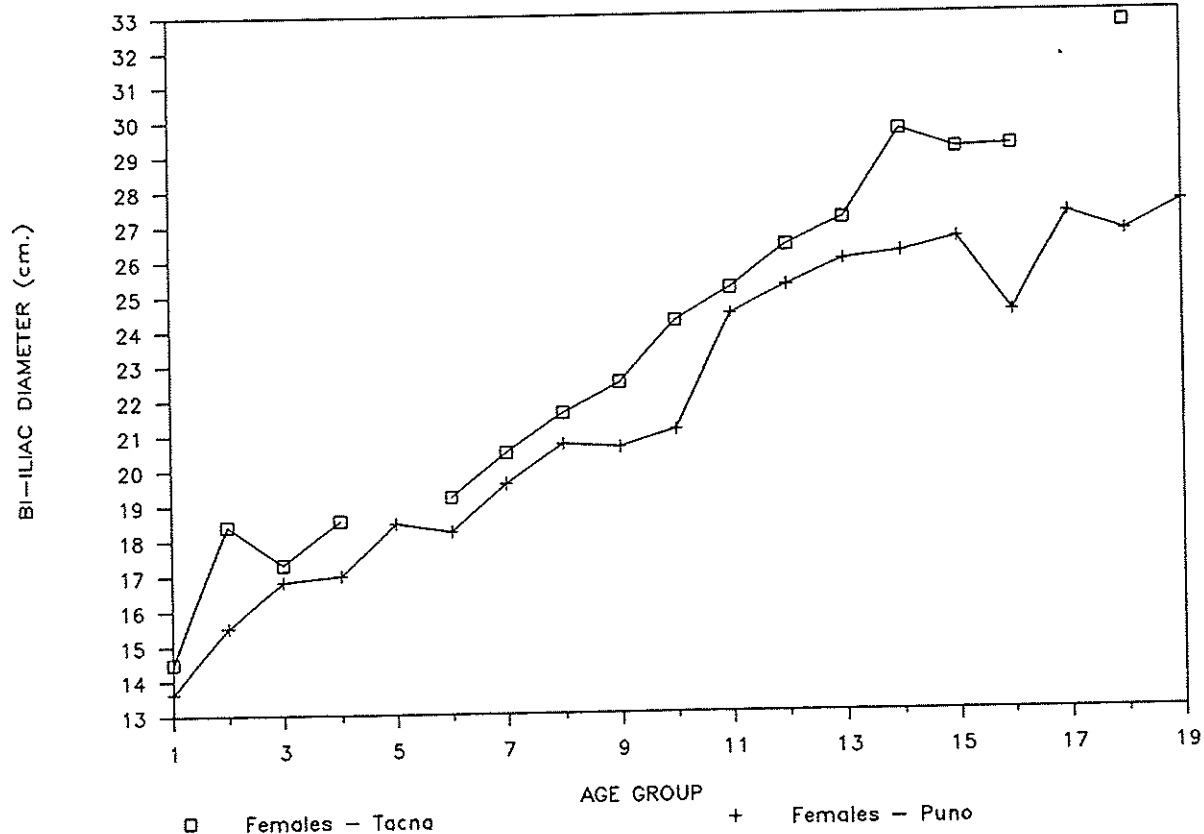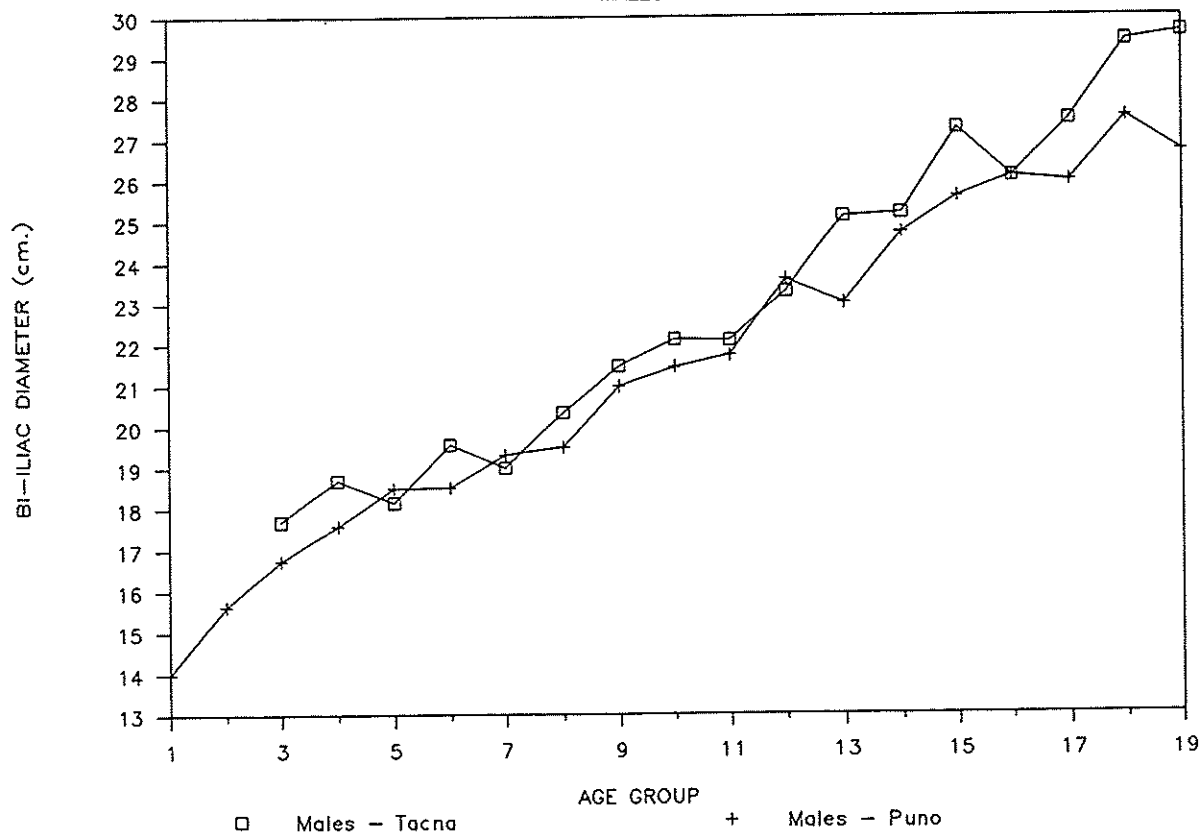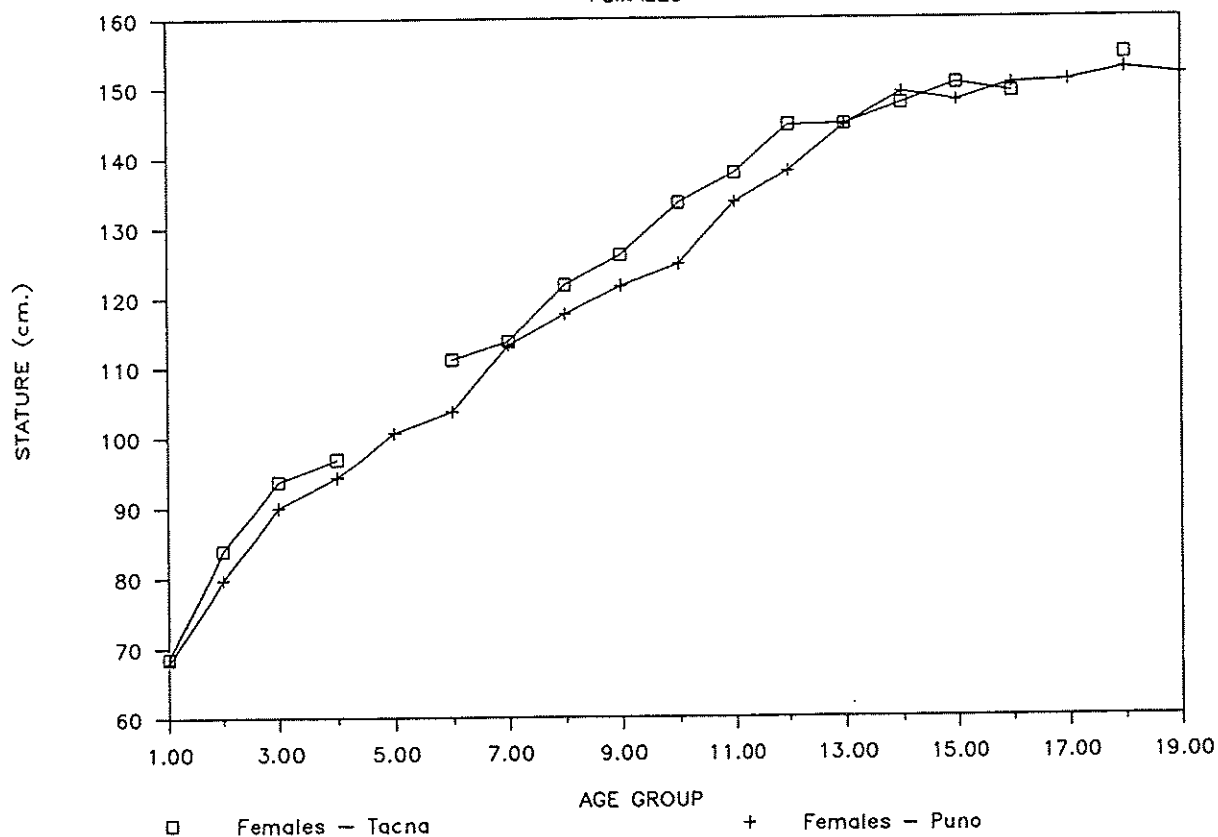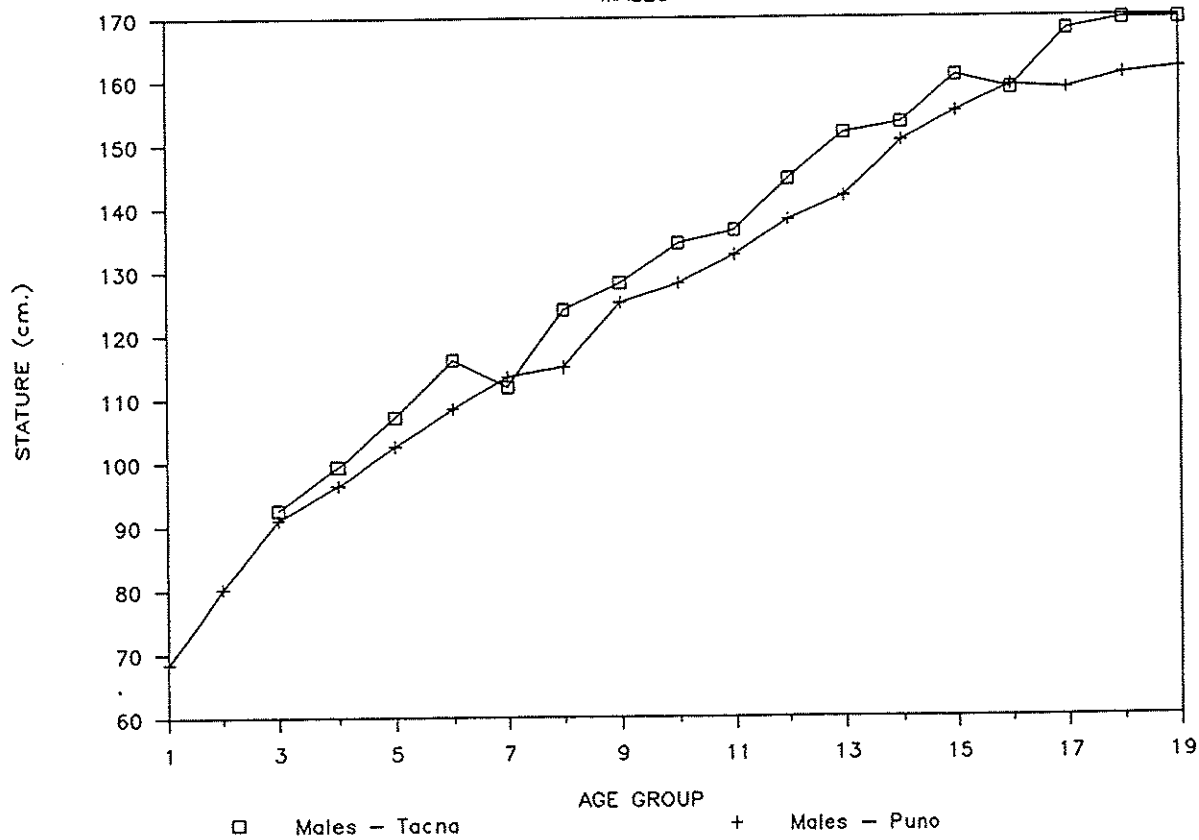
MIDAXILLARY SKINFOLD

FEMALES

Females — Tacna   +   Females — Puno
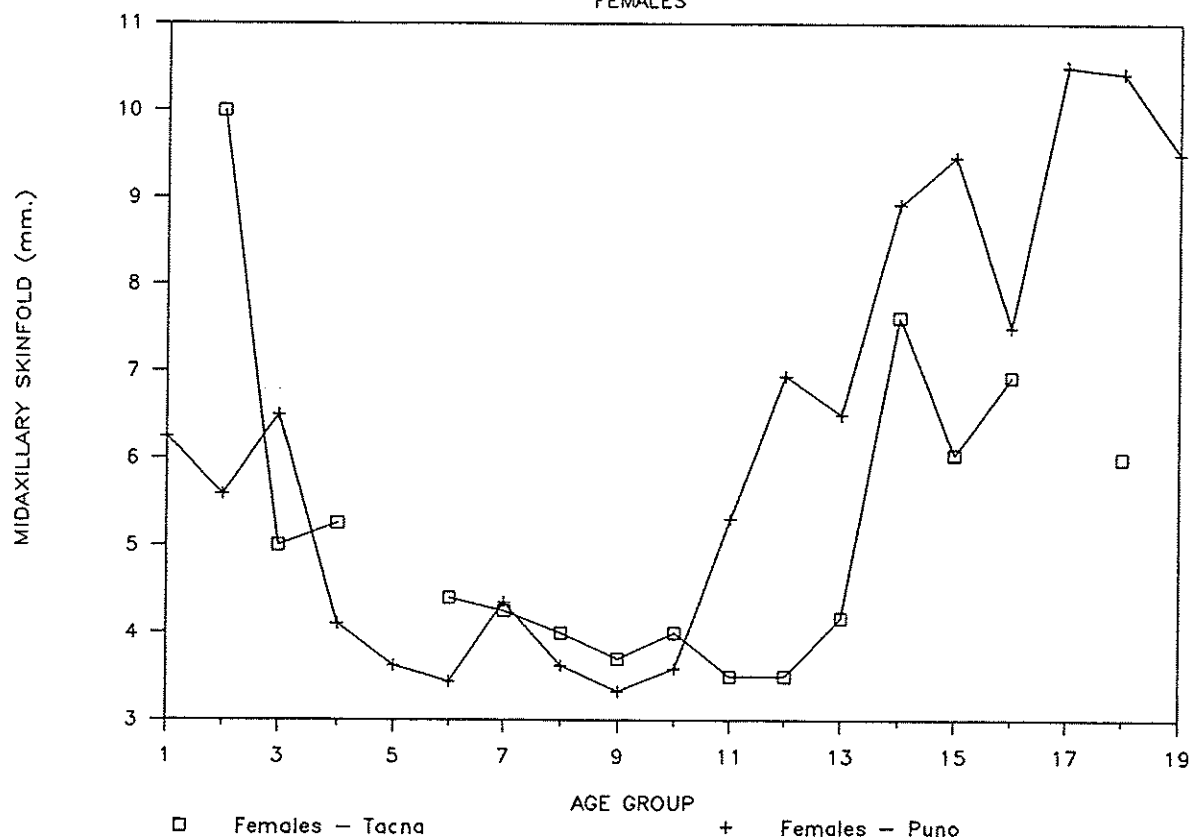
MIDAXILLARY SKINFOLD

MALES

Males — Tacna   +   Males — Puno
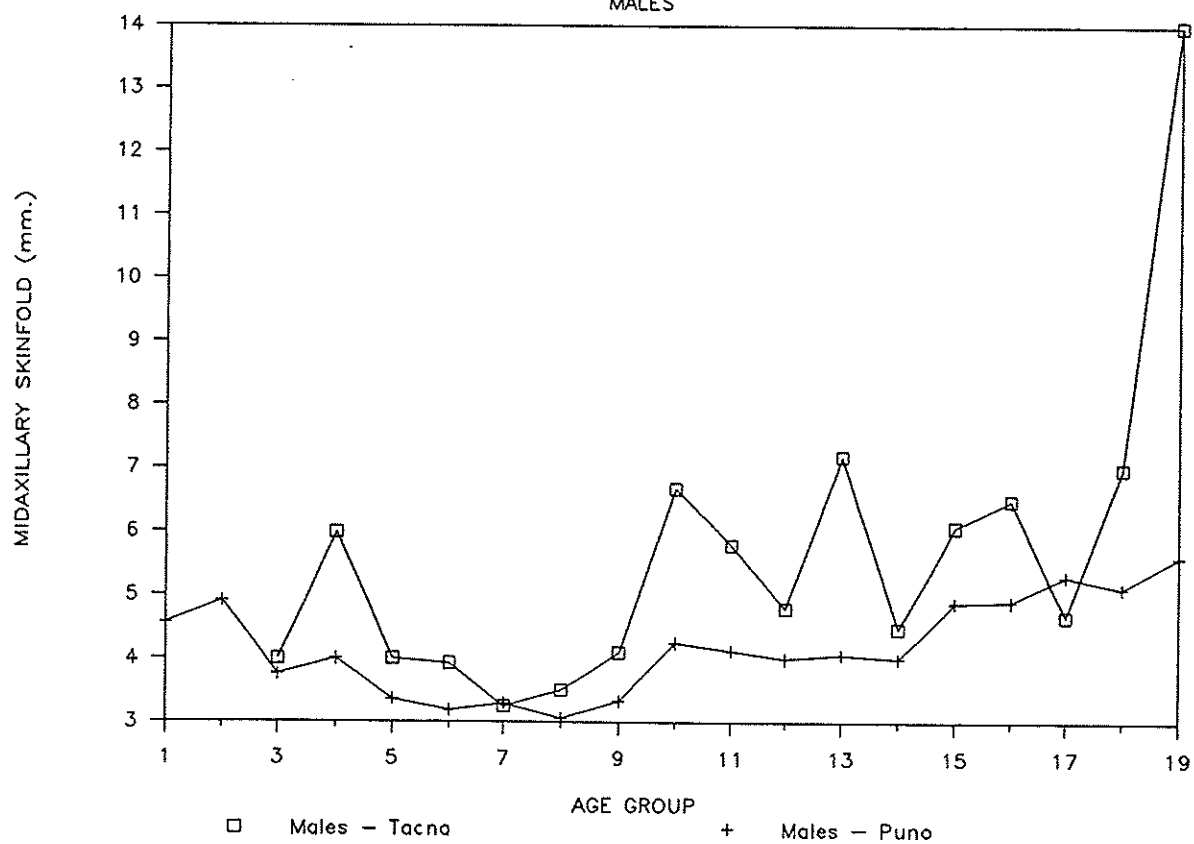
CHEST CIRCUMFERENCE – SUBSTERNAL

FEMALES
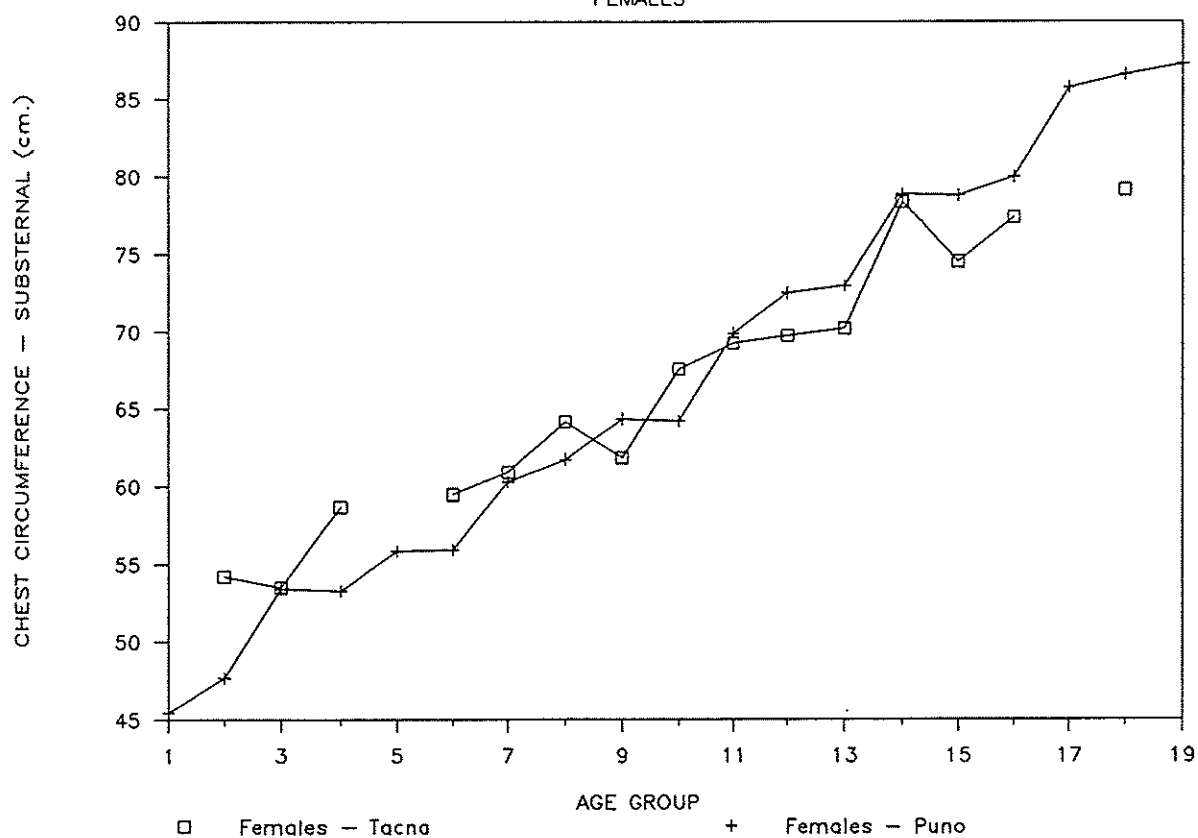
CHEST CIRCUMFERENCE – SUBSTERNAL

MALES
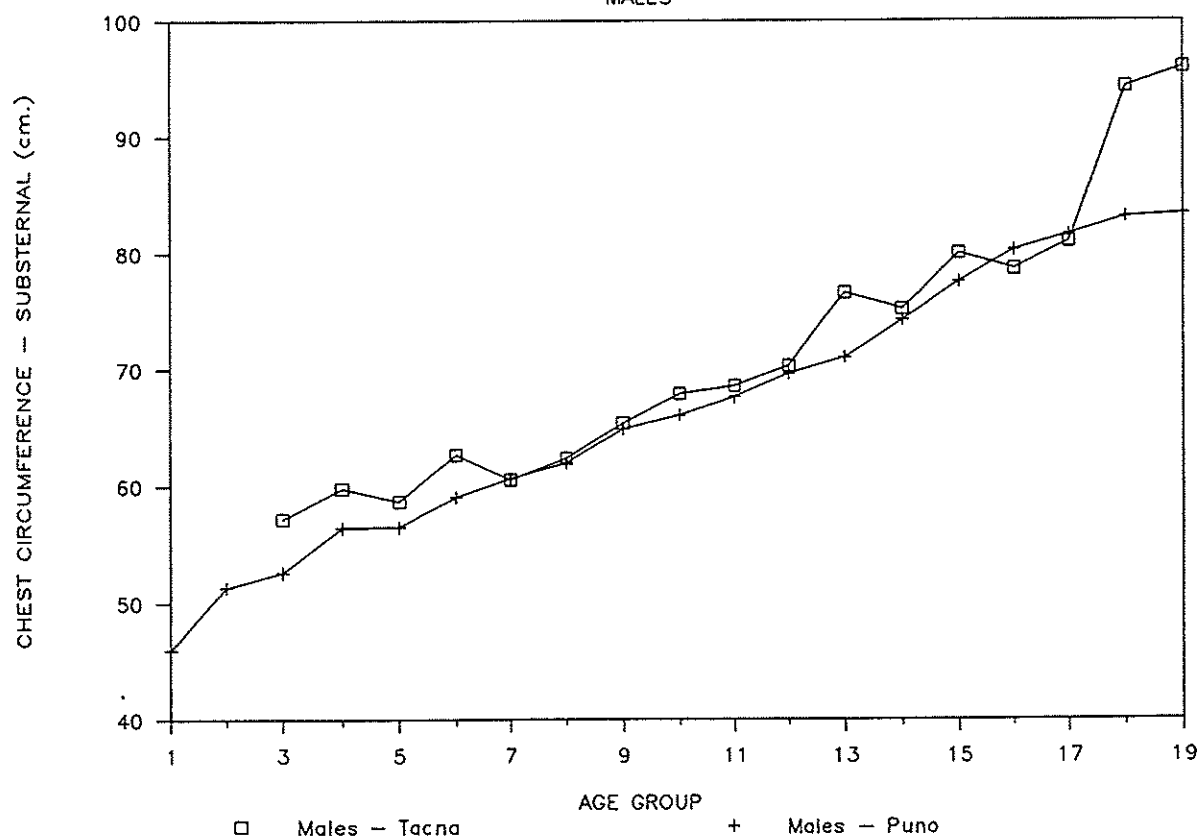
SITTING HEIGHT

FEMALES
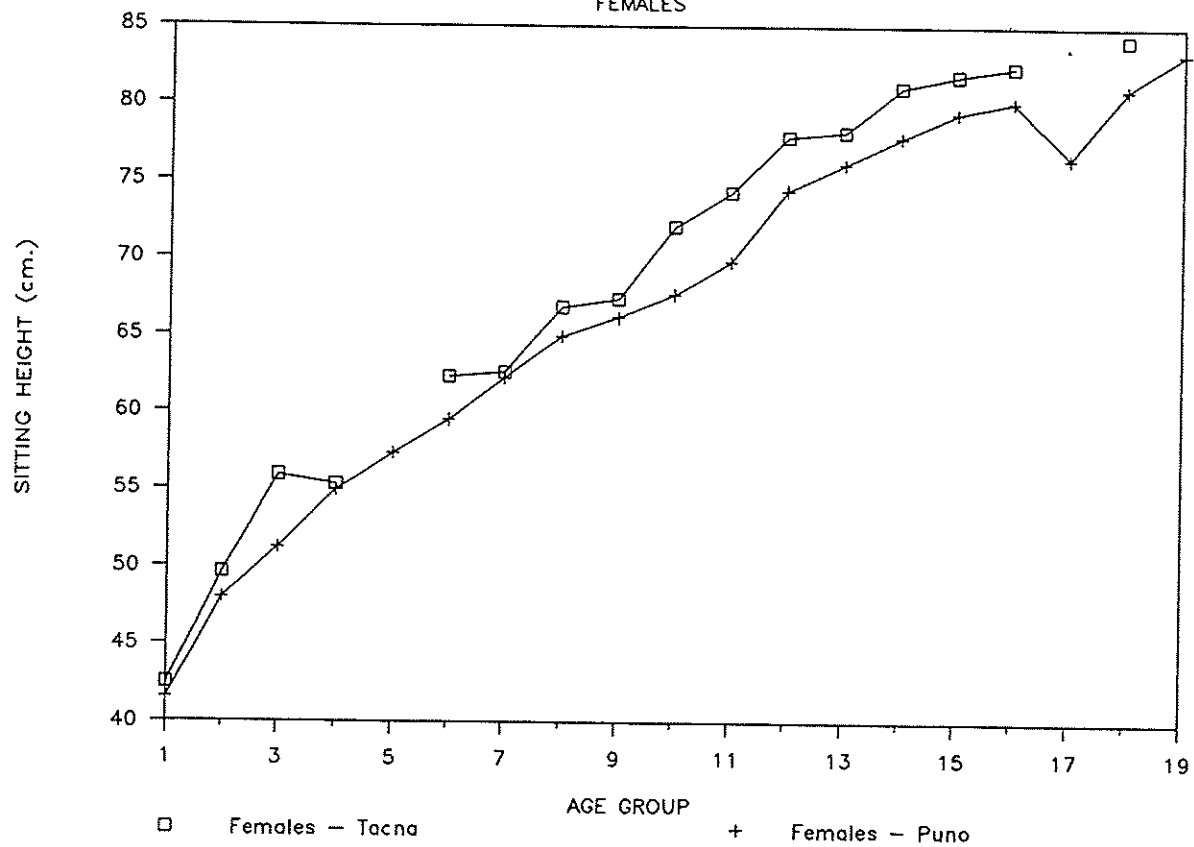
AGE GROUP

□ Females — Tacna   +   Females — Puno

SITTING HEIGHT

MALES

AGE GROUP

□   Males — Tacna   +   Males — Puno

SUPRAILIAC SKINFOLD

FEMALES

□ Females — Tacna   + Females — Puno

SUPRAILIAC SKINFOLD

MALES

□ Males — Tacna   + Males — Puno
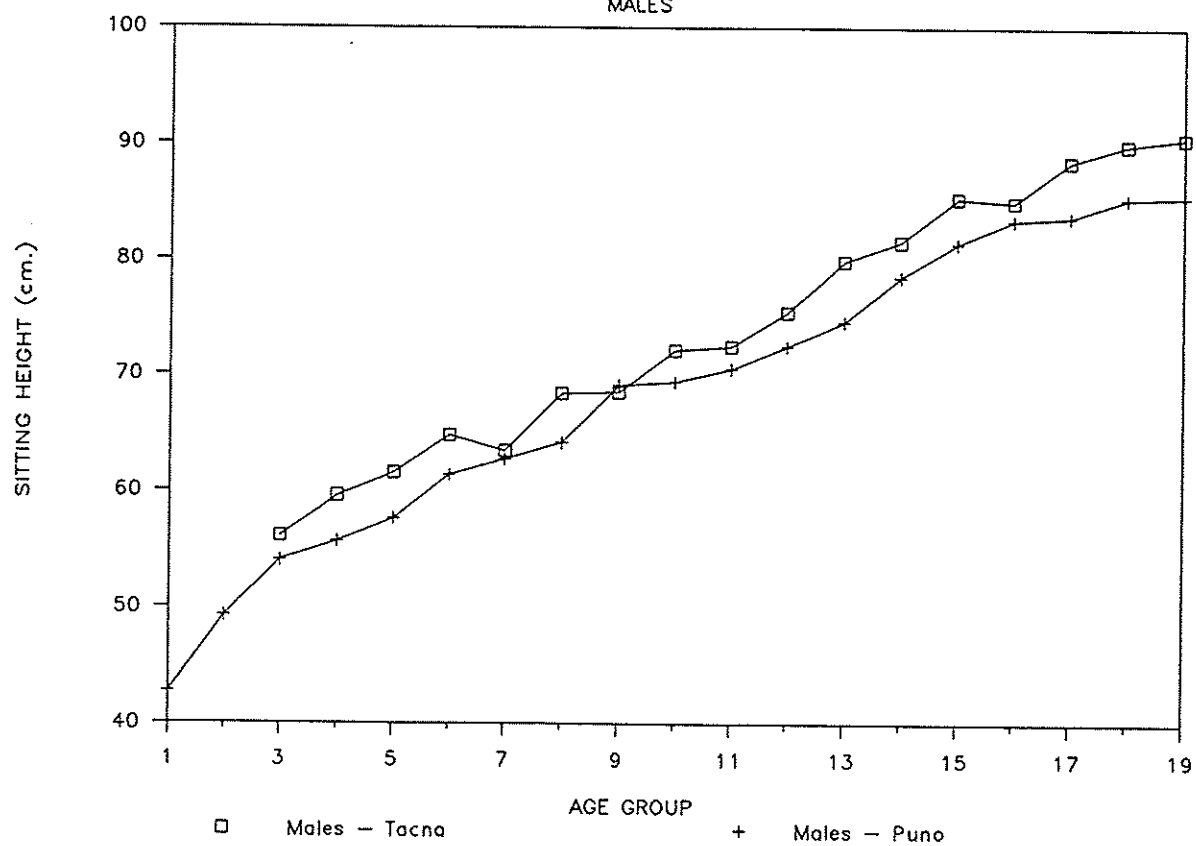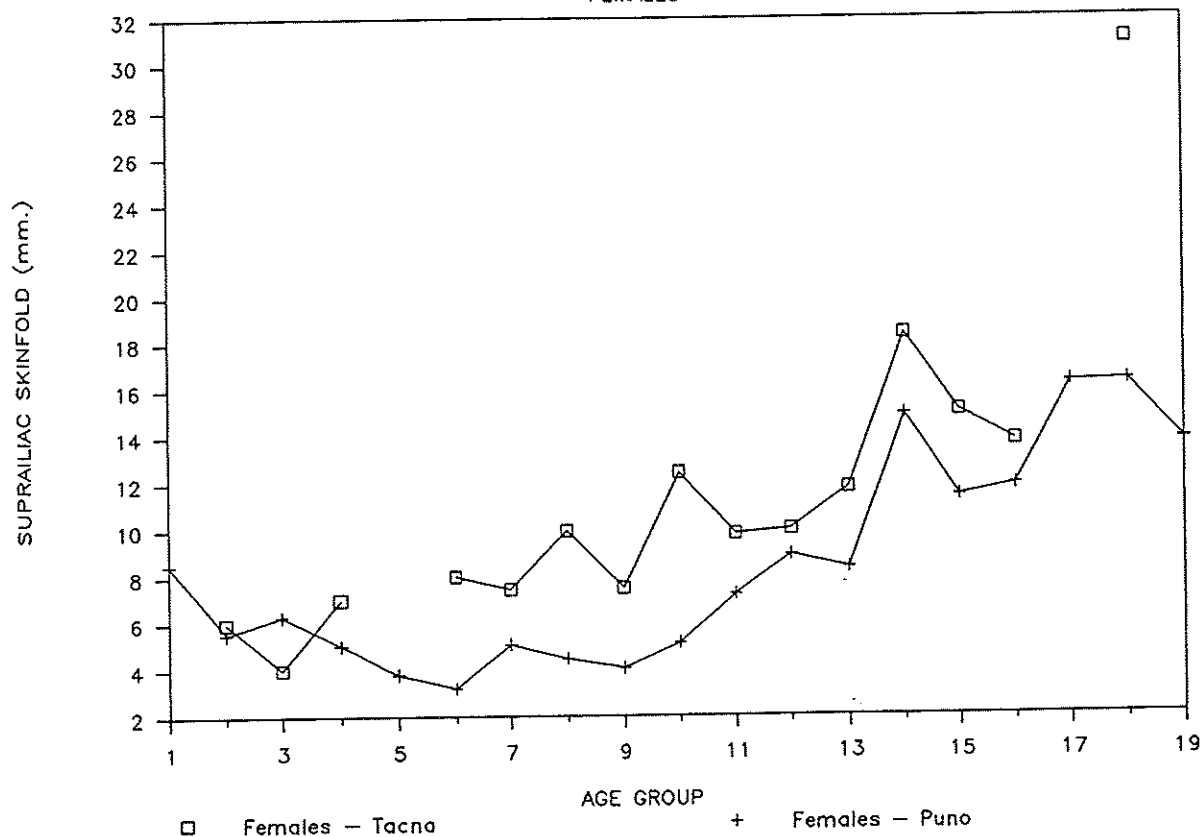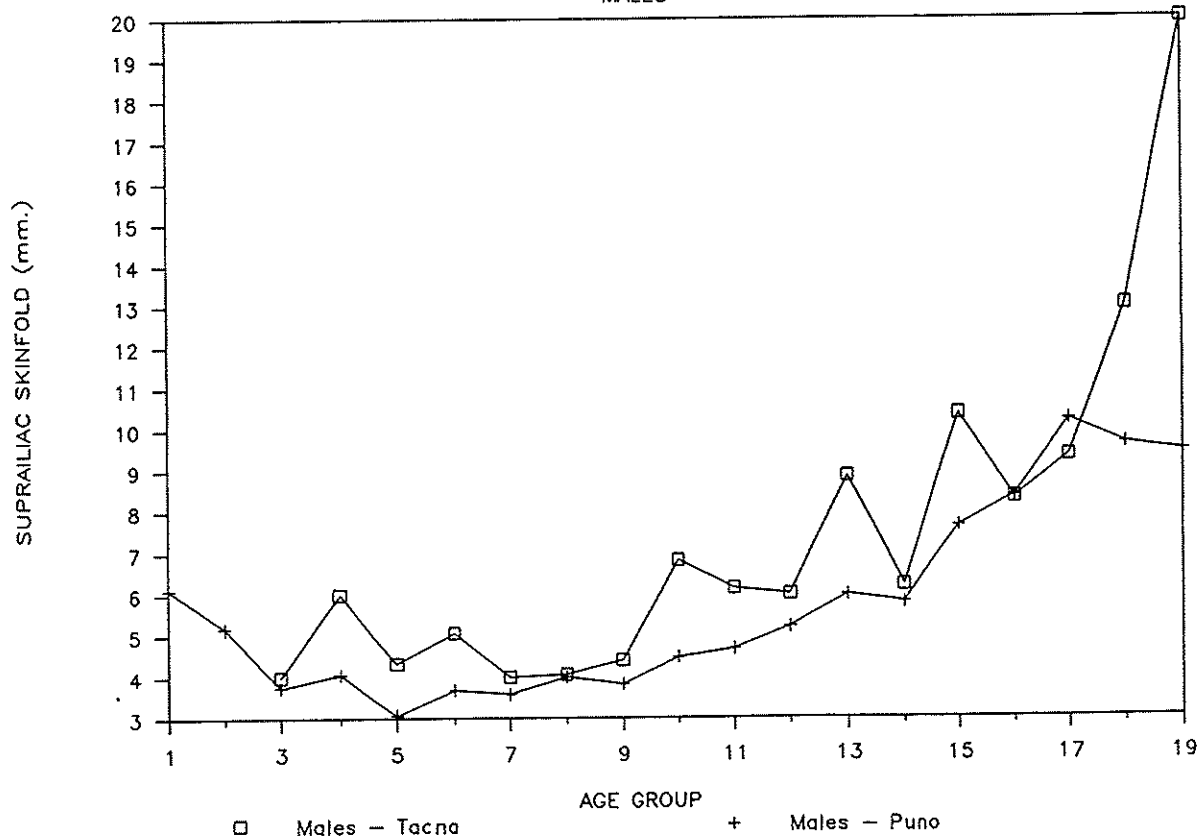
SUBSCAPULAR SKINFOLD

FEMALES
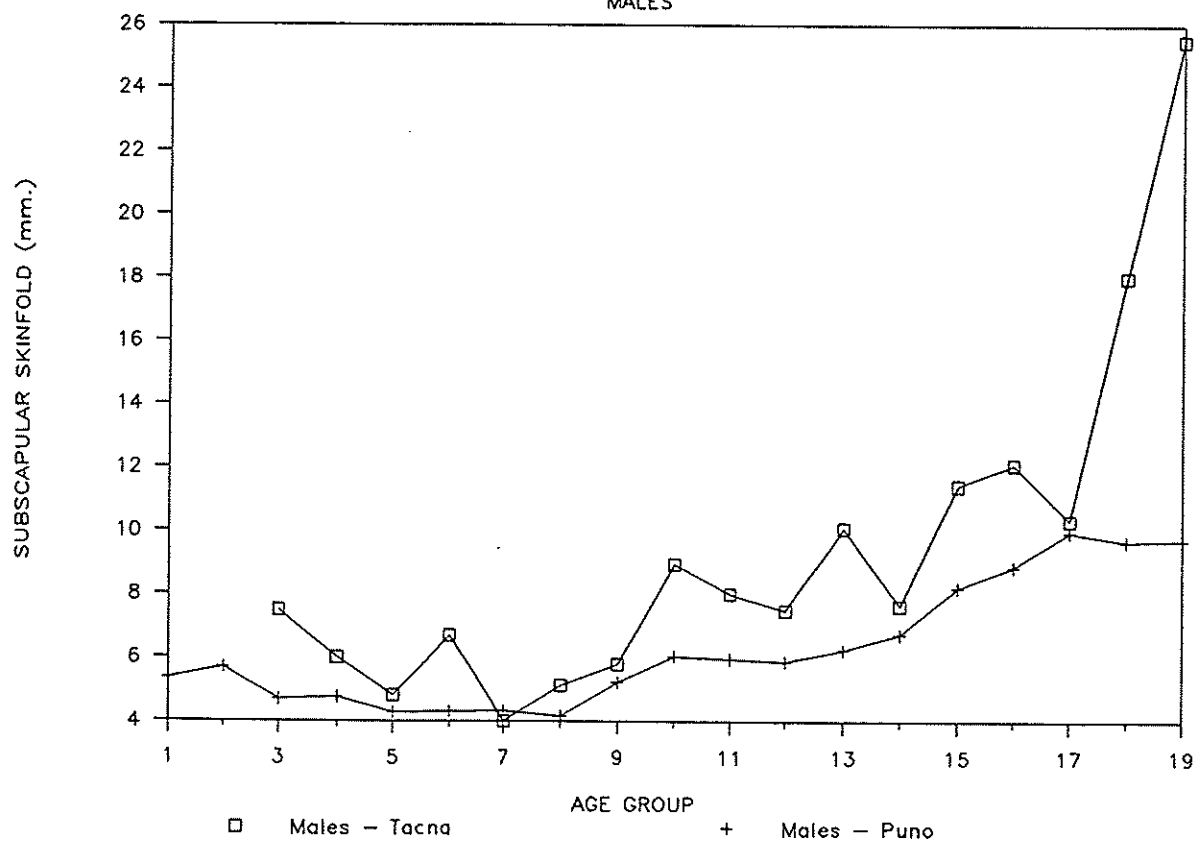
□   Females — Tacna   +   Females — Puno

SUBSCAPULAR SKINFOLD

MALES

□   Males — Tacna   +   Males — Puno

STERNAL LENGTH

FEMALES
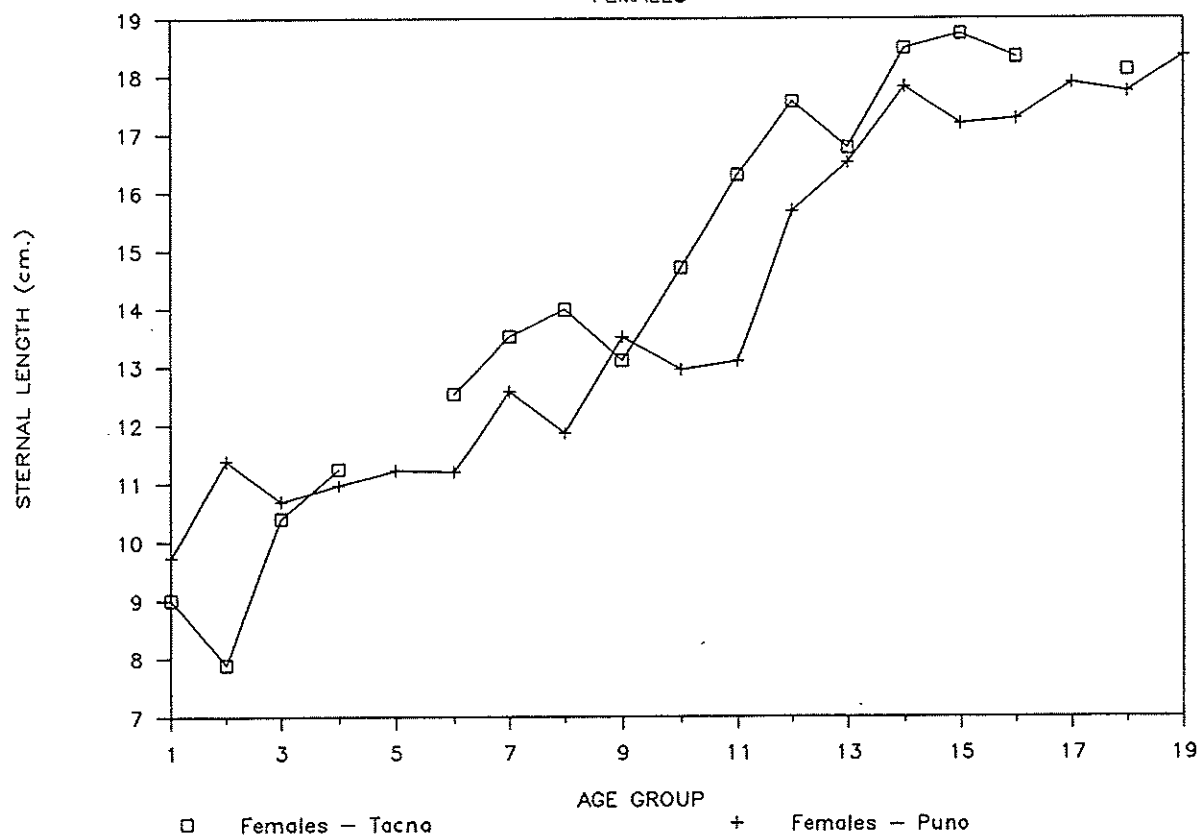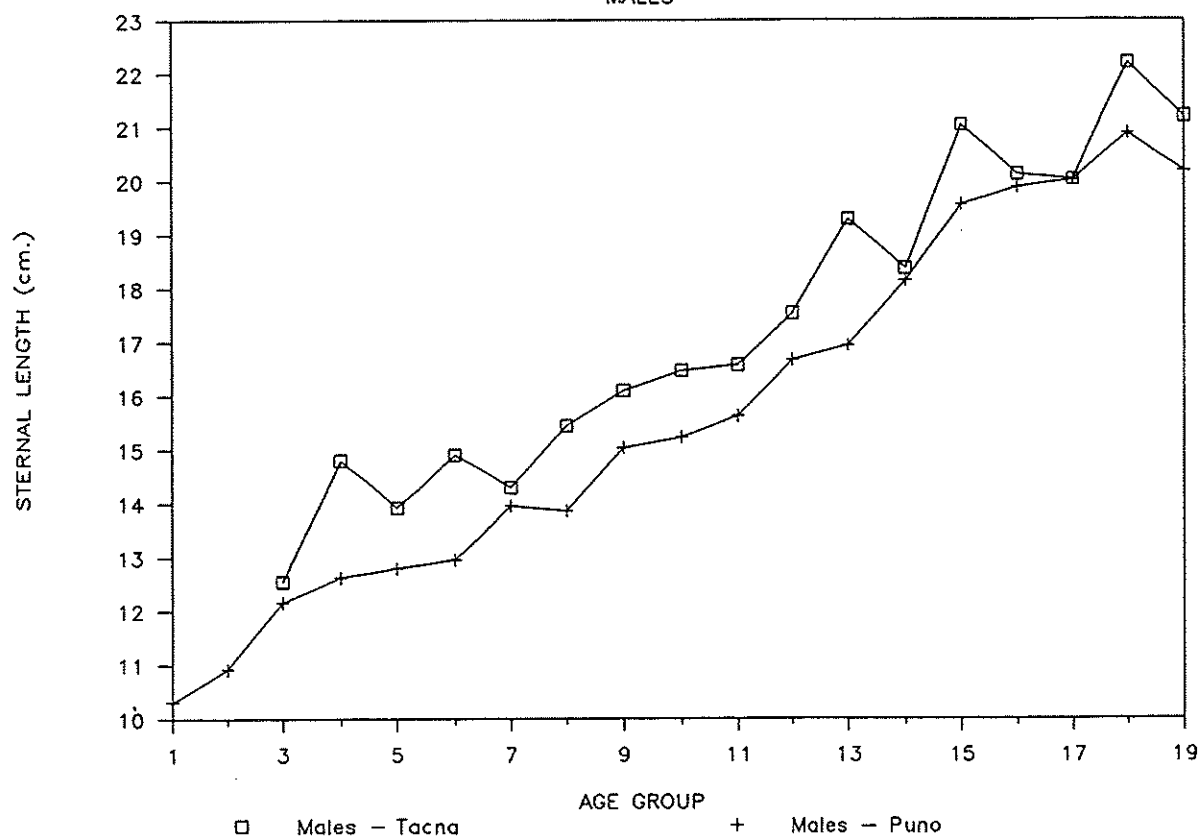
AGE GROUP

□   Females — Tacna   +   Females — Puno

STERNAL LENGTH

MALES

AGE GROUP

□   Males — Tacna   +   Males — Puno

CHEST CIRCUMFERENCE — FORCED EXP.
FEMALES
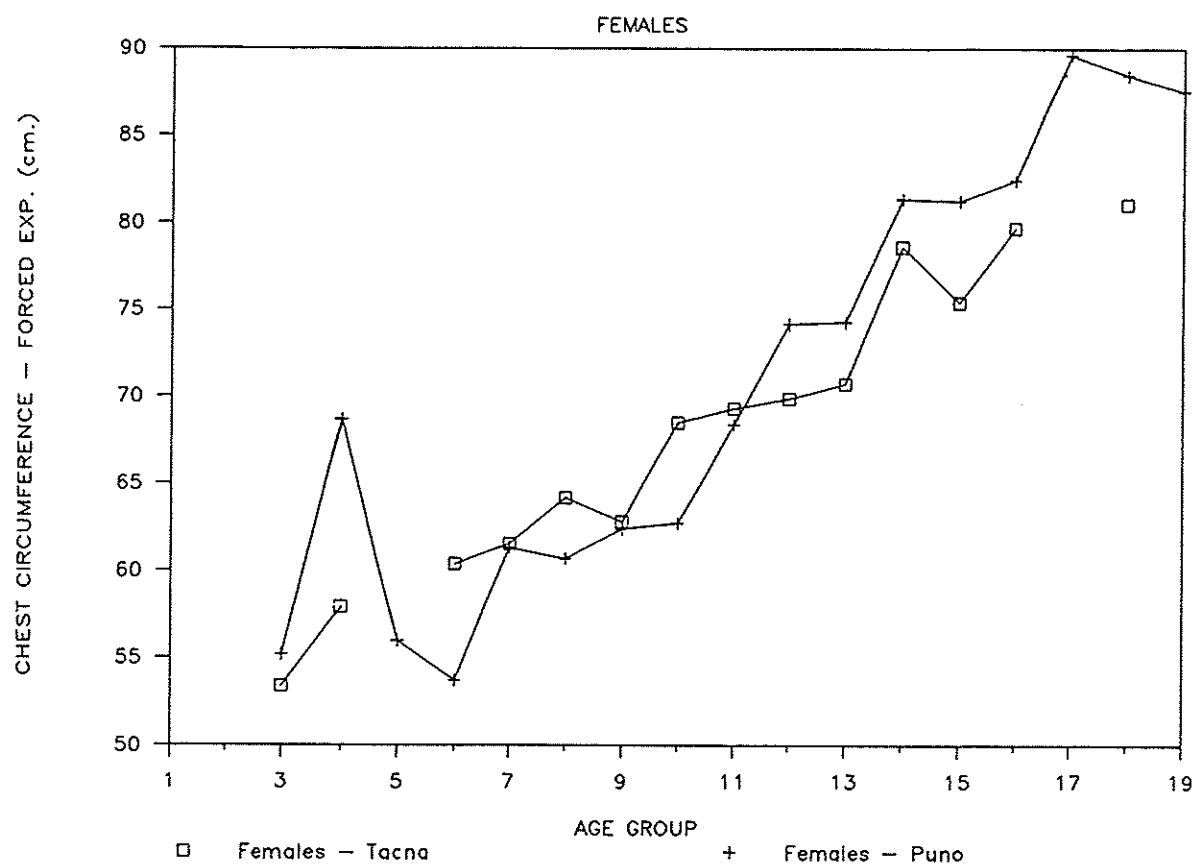
CHEST CIRCUMFERENCE — FORCED EXP.
MALES
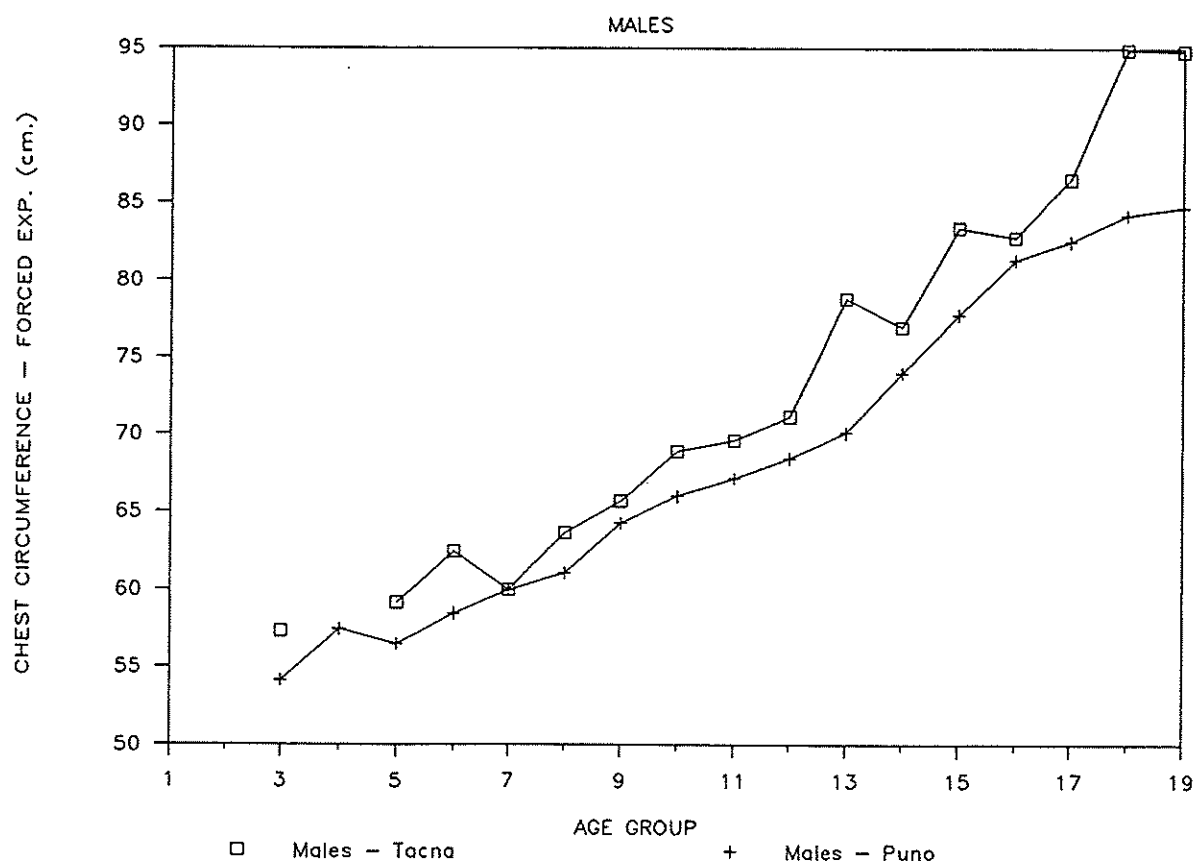
CHEST CIRCUMFERENCE — FORCED INSP.
FEMALES
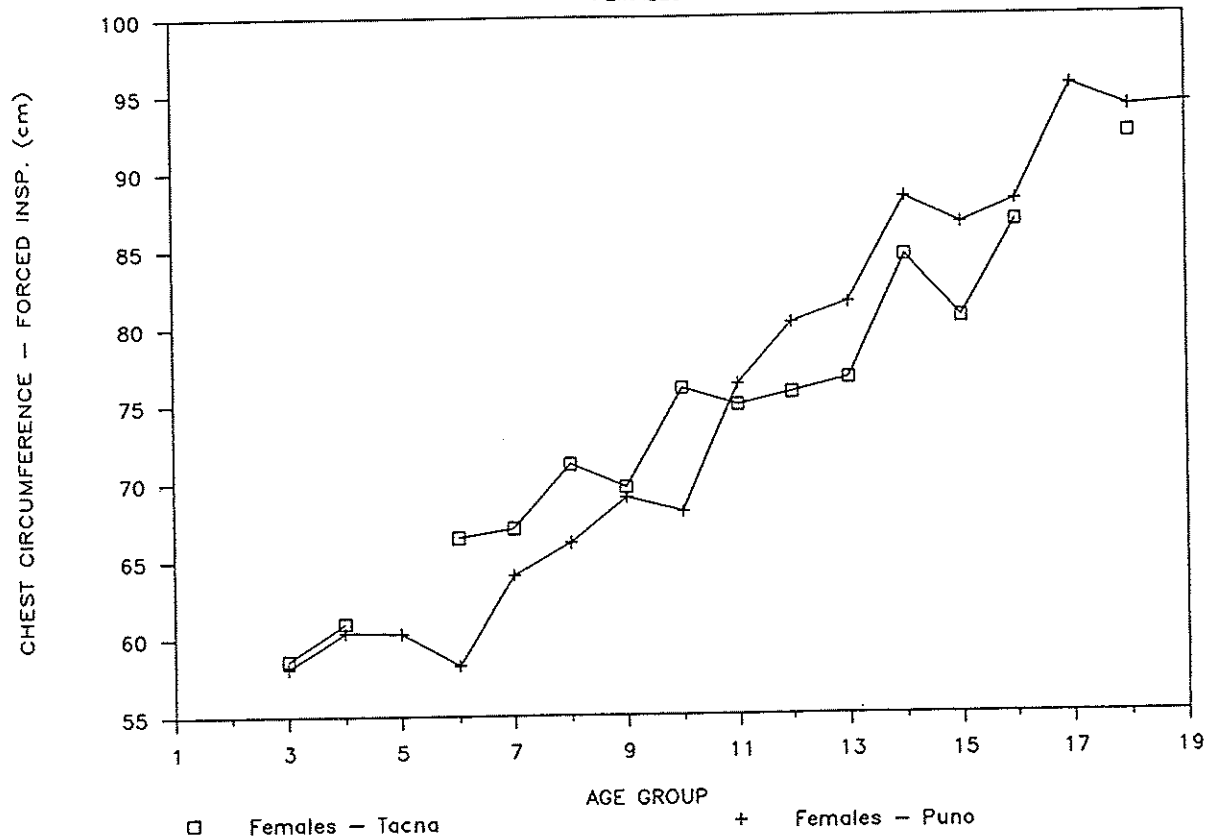
CHEST CIRCUMFERENCE — FORCED INSP.
MALES

CHEST CIRCUMFERENCE

FEMALES

AGE GROUP

□ Females – Tacna   +   Females – Puno

CHEST CIRCUMFERENCE

MALES

AGE GROUP

□ Males – Tacna   +   Males – Puno
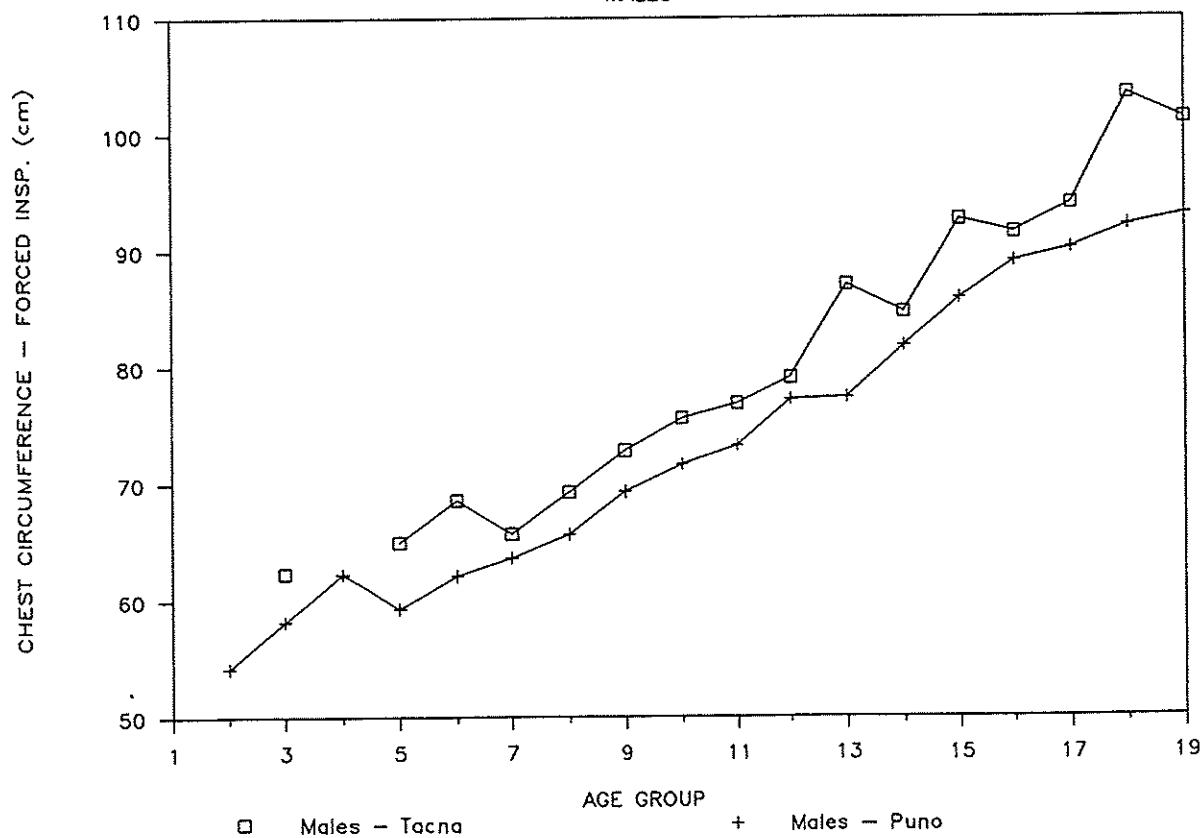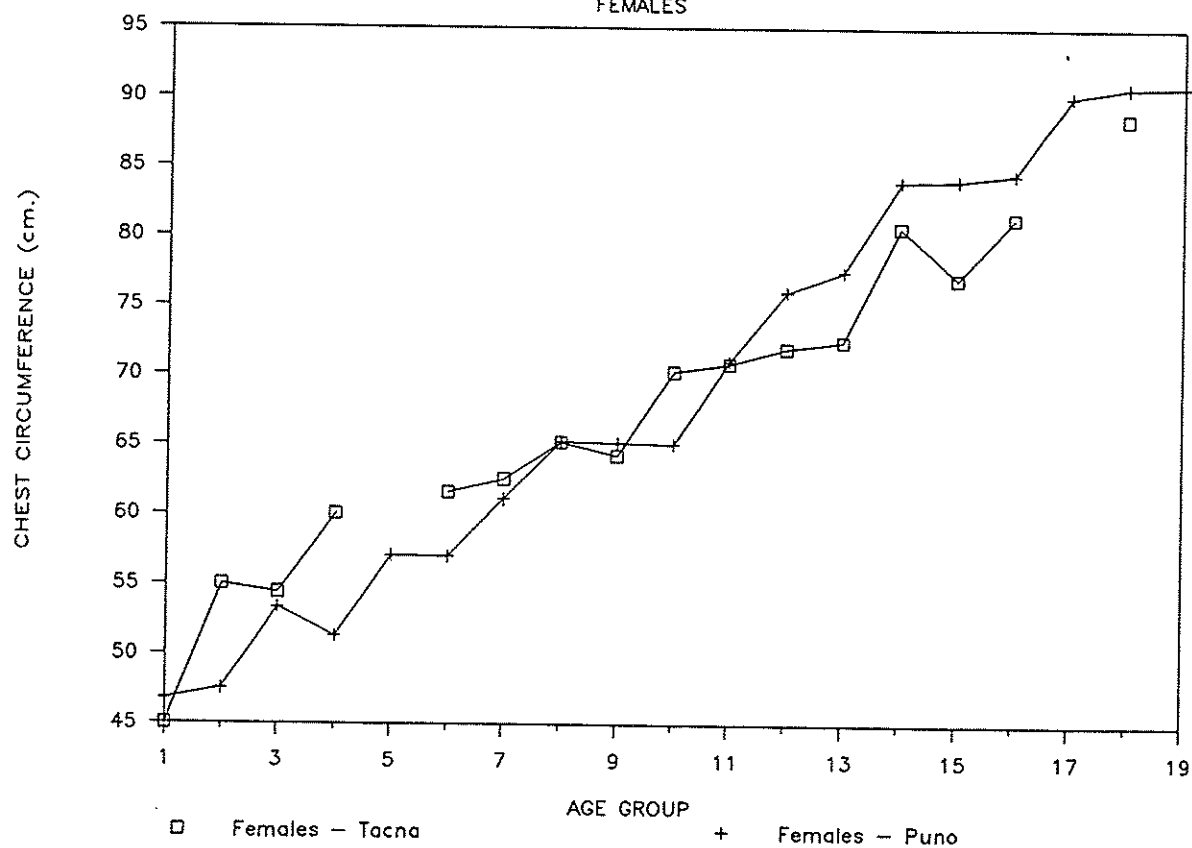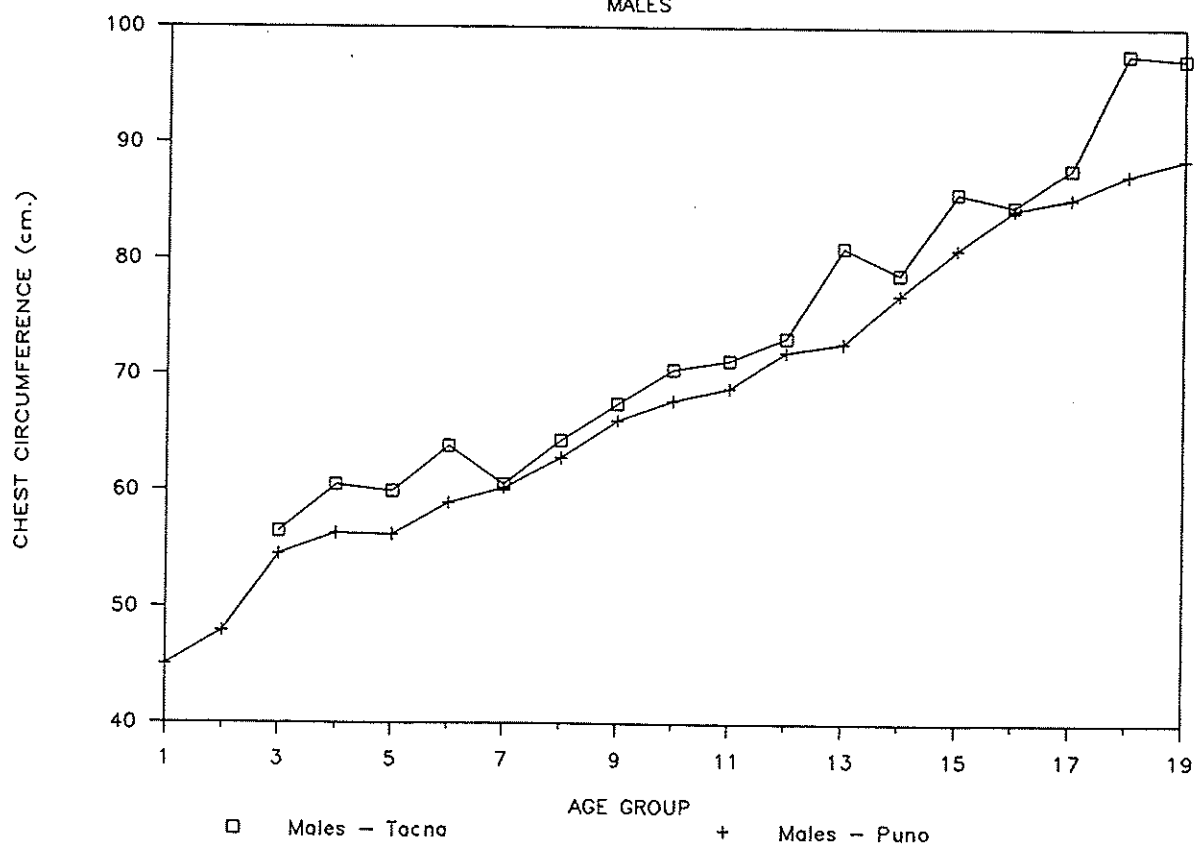
TRANSVERSE DIAMETER
FEMALES

Females — Tacna   +   Females — Puno
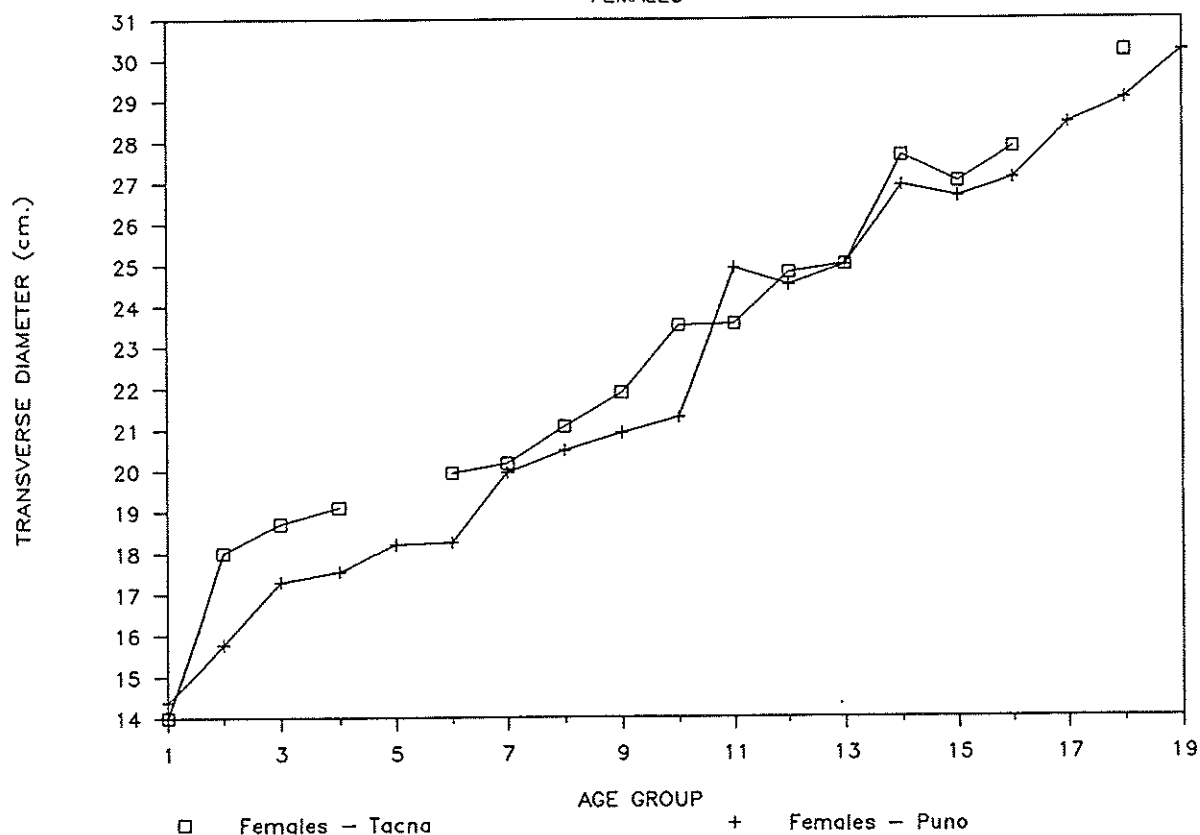
TRANSVERSE DIAMETER
MALES

Males — Tacna   +   Males — Puno
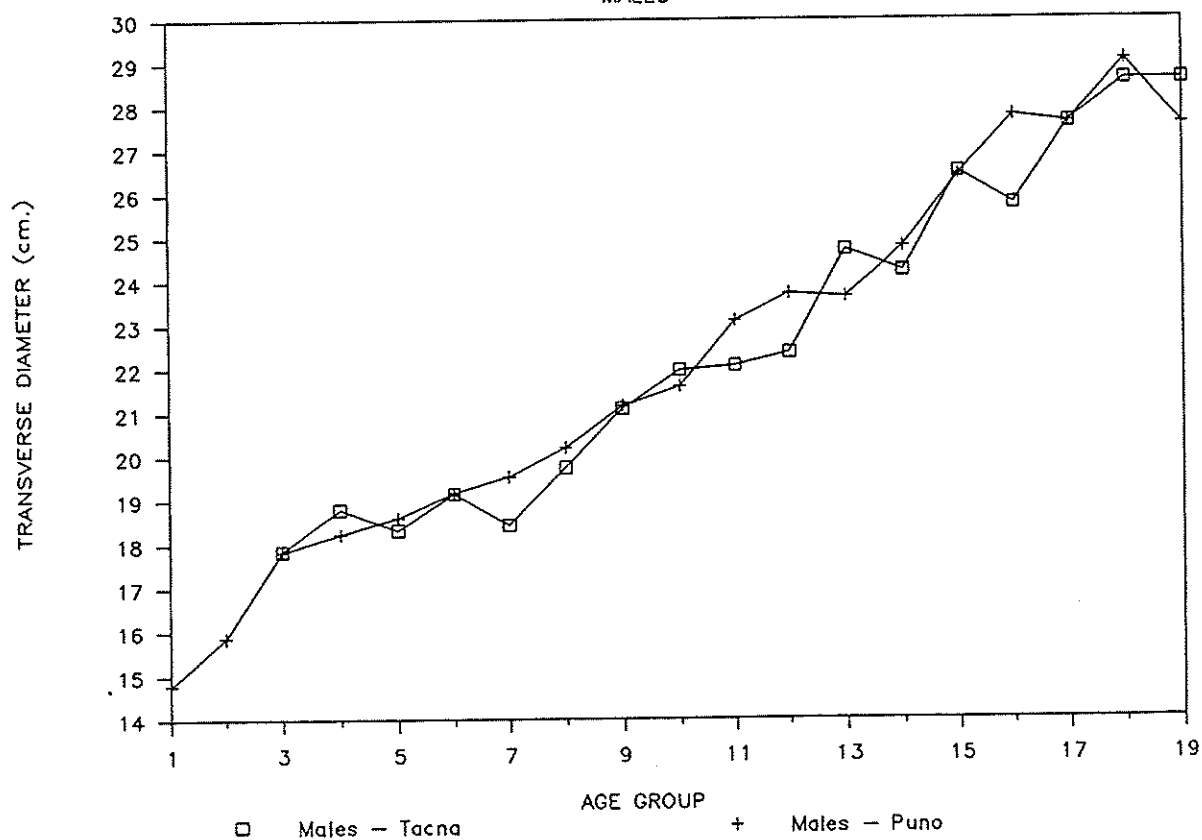
TRICEPS SKINFOLD

FEMALES

□   Females — Tacna   +   Females — Puno
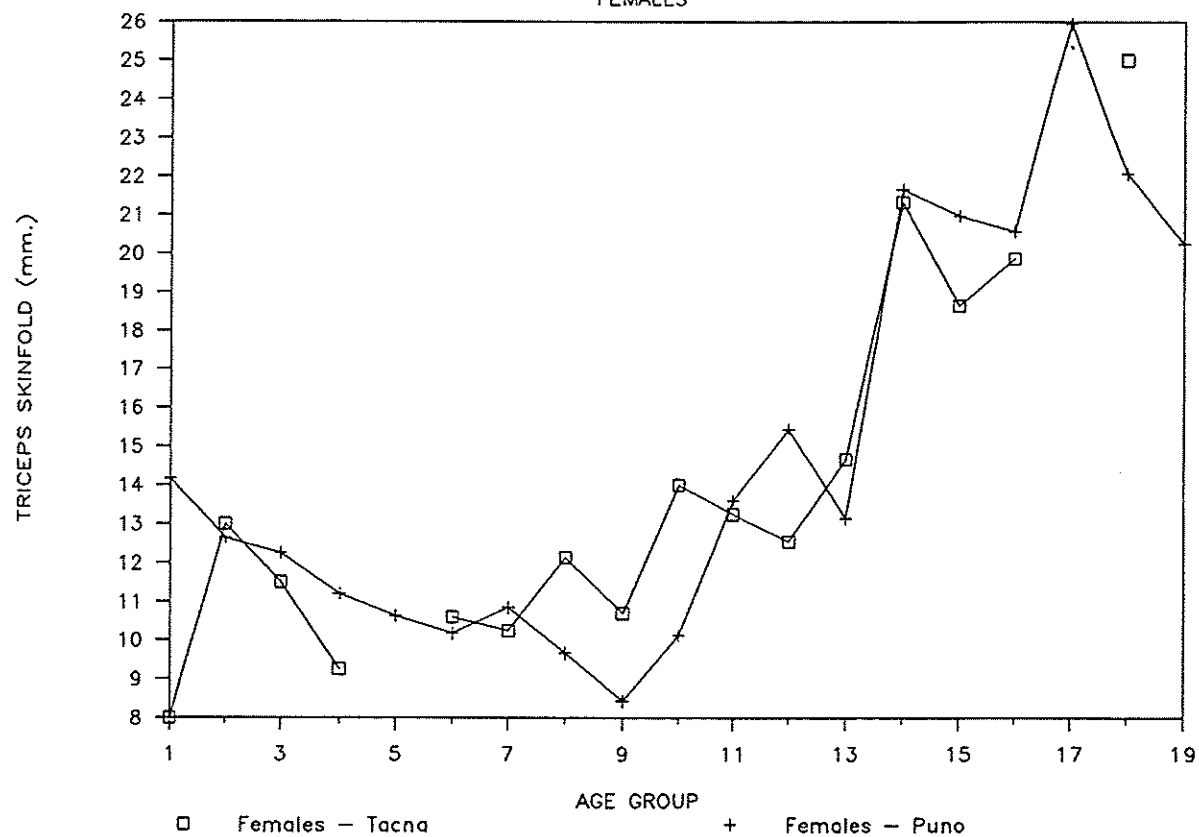
TRICEPS SKINFOLD

MALES

□   Males — Tacna   +   Males — Puno
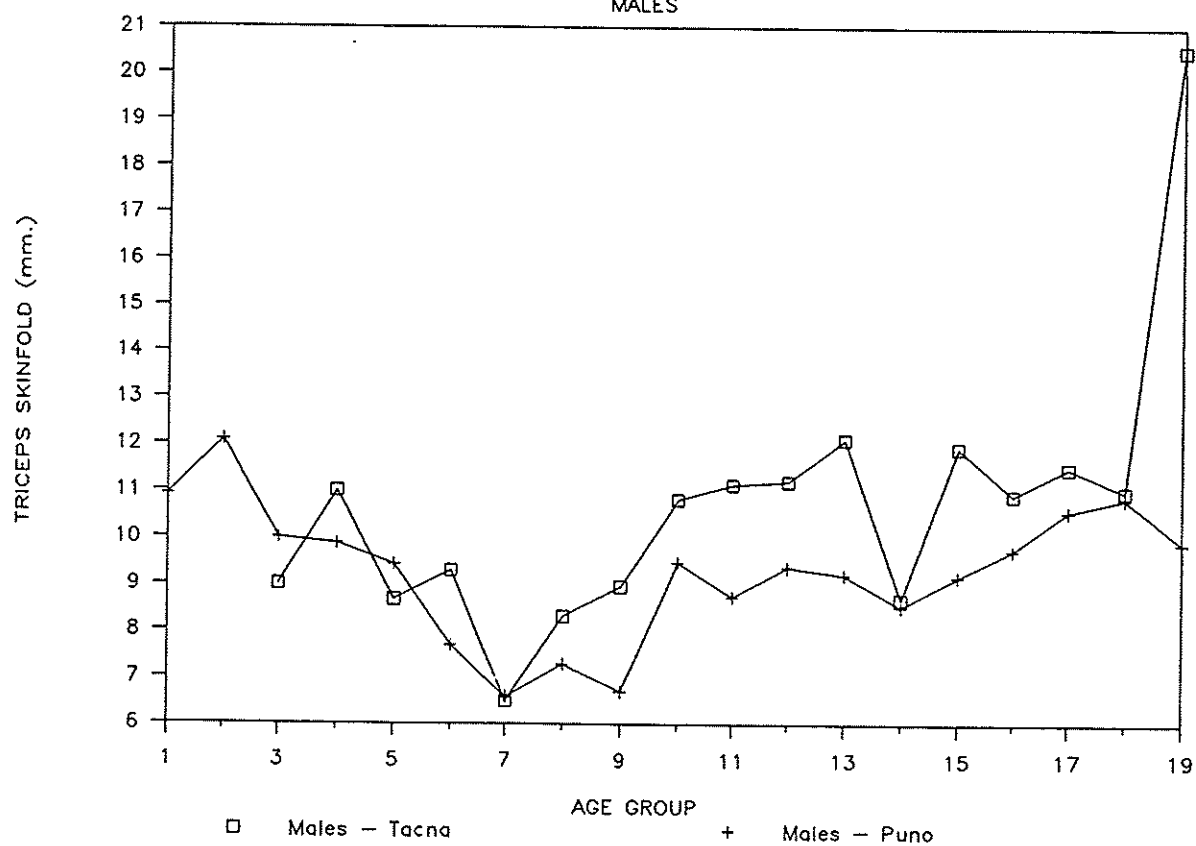
UPPER ARM CIRCUMFERENCE
FEMALES

UPPER ARM CIRCUMFERENCE
MALES

WEIGHT
FEMALES

□   Females — Tacna   +   Females — Puno
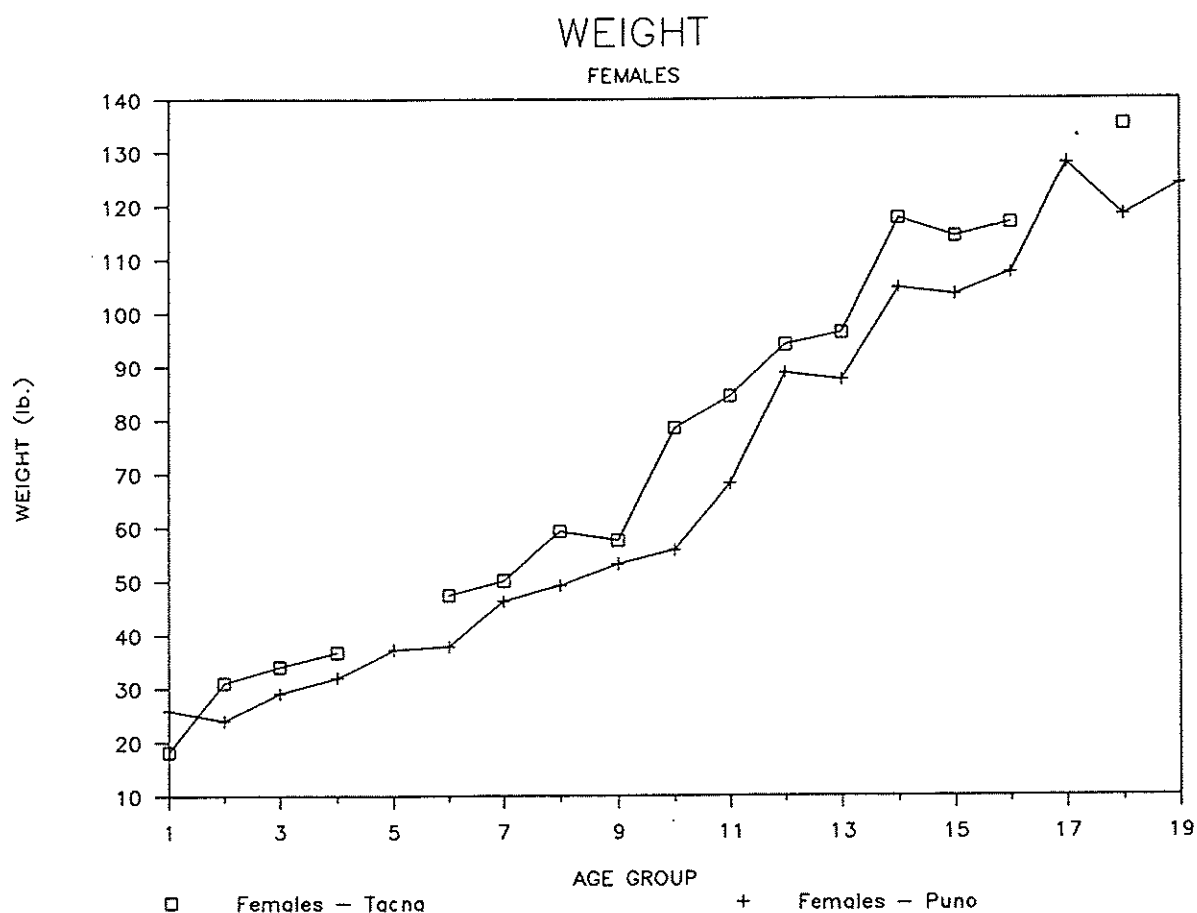
WEIGHT
MALES

□   Males — Tacna   +   Males — Puno
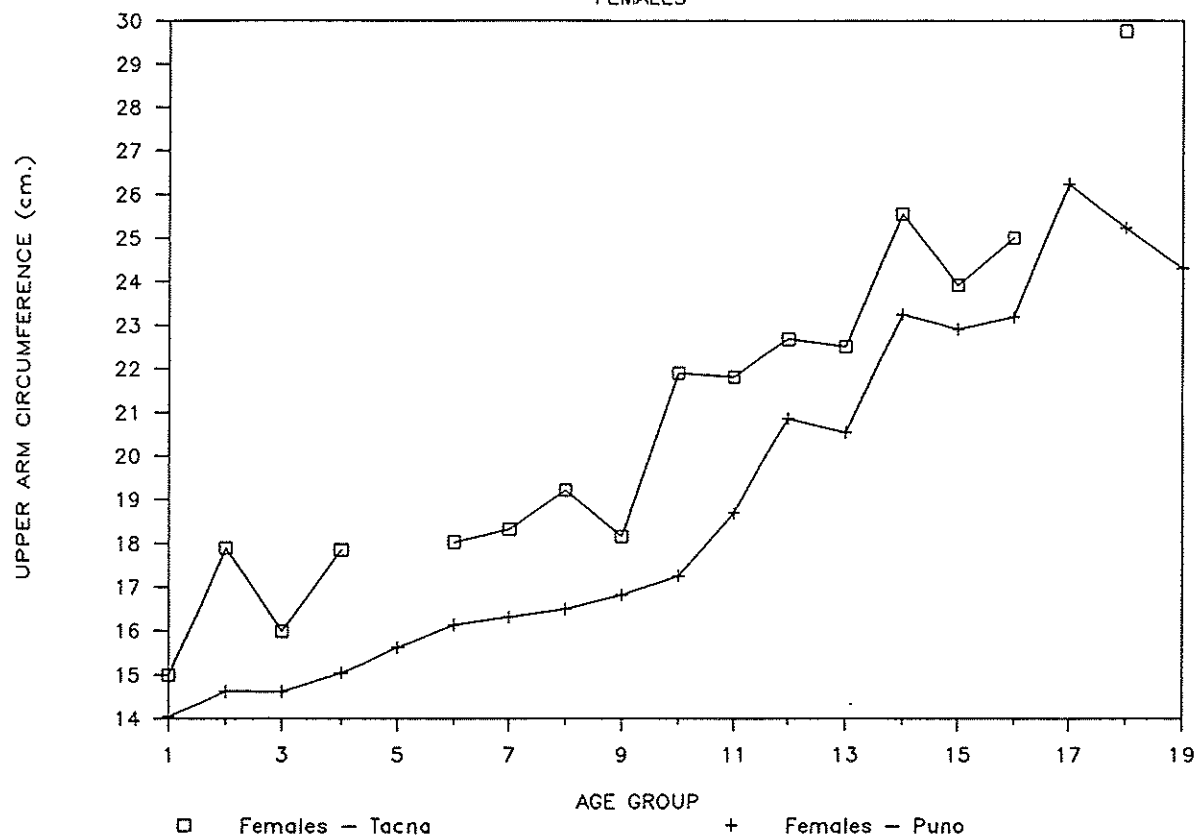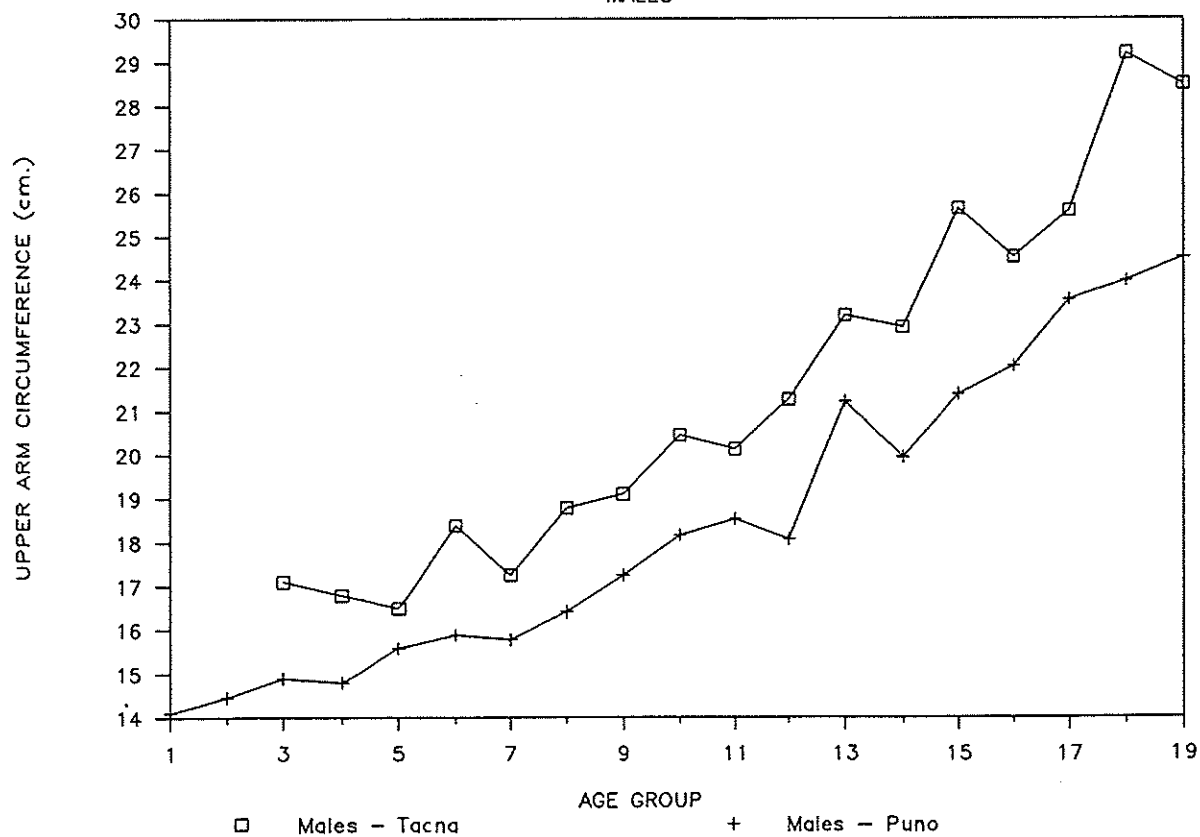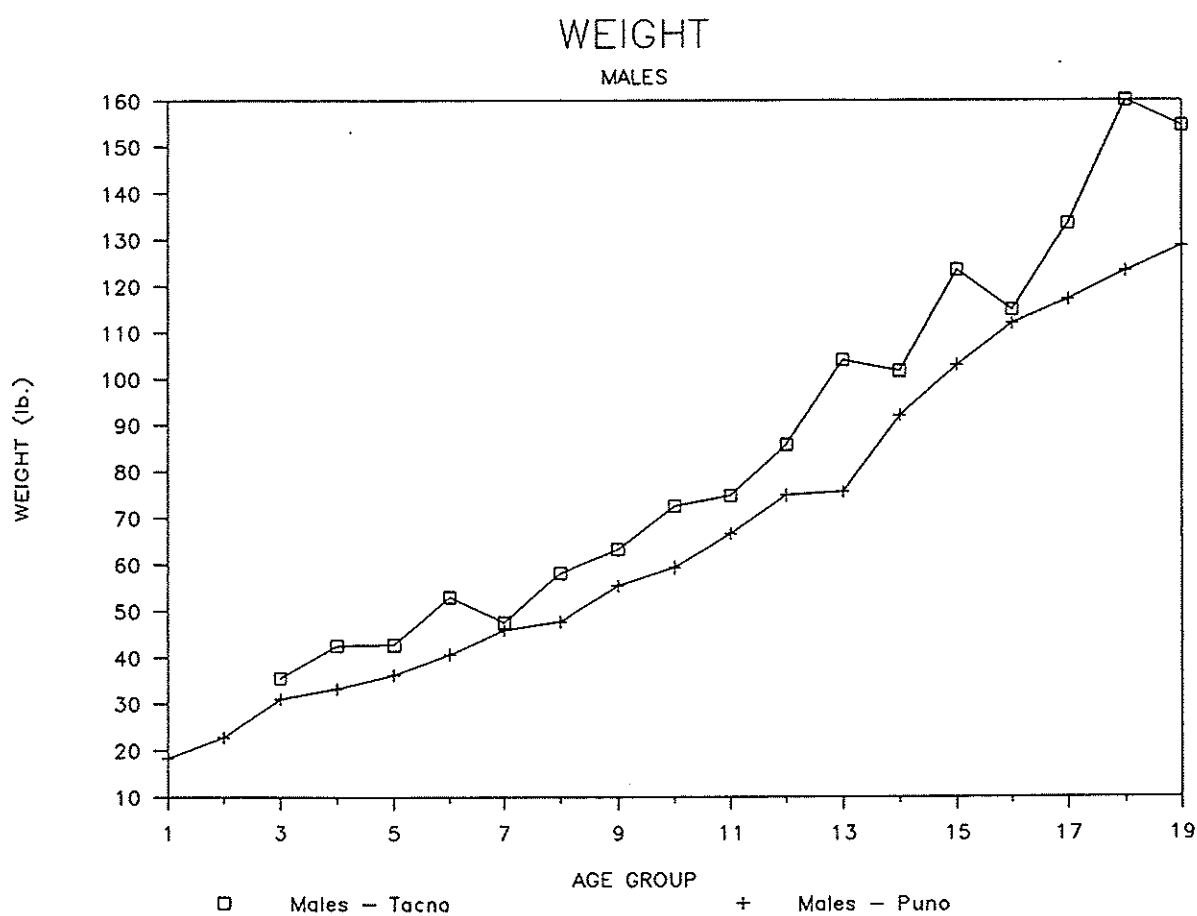
CHAPTER 9

A COMPARATIVE OVERVIEW OF SOME RECENT RESEARCH ON ADAPTATION AND EVOLUTION OF ANDEAN POPULATIONS

Robert B. Eckhardt

The seven chapters that comprise the empirical core of this monograph deal directly (the studies by Kramer, Vandemark, Ahn, and Melton) or indirectly (the studies by Whittaker and Lincoln) with the central question that was addressed at the outset of the project: is there any evidence for a genetic component influencing the morphological variations that have long been recognized as characteristic of Andean highlanders?

In working toward an answer to this question, three studies--in chronological order of their original completion, by Kramer (Chapter 2 here), Vandemark (Chapter 5), and the first contribution by Ahn (Chapter 6)-- applied a common methodology, based upon some rather straightforward quantitative genetic approaches such as heritability analysis of parent-offspring and sib data, to the single large body of anthropometric measurements collected during the 1978 field season in Camacani. One of the major findings that emerged from these related analyses was the realization that there was an evident pattern observable in the set of heritability estimates: the values for overall physical size (such as stature and body weight) exhibited higher heritabilities than those for thoracic dimensions (such as sternal length and the various transverse and anterior-posterior thoracic diameters).

These results, which we began to report within two years of data collection in 1978, were interpreted as being consistent with (though not yet definitive proof of) the idea that selection could have operated to increase thoracic volumes. A logical concomitant of any shift in the mean values for thoracic dimensions would have been a reduction in the additive genetic variation in the population. This reduction in variance would simply be a natural consequence of elimination from the population of whatever genes were associated with the development of smaller chest dimensions. Since heritability estimates the fraction of the total phenotypic variance that is attributable to genotypic variation (or, more narrowly, to additive genetic variation), all other things being equal, if selection acted to increase the mean it would lower the variance and, necessarily, heritability. Of course, given the definition of heritability, other combinations of effects could produce outcomes that might appear superficially the same. Hence, if the range of potential explanations for the observed patterns were to be narrowed to a focus on selection, other evidence would be needed.

Ahn's subsequent work (Chapter 7 here) took a more ambitious and sophisticated approach, using a multivariate method to detect the direction and magnitude of selection. The results from the resultant analysis of the Camacani data showed that for traits representing general body size, intermediate phenotypic values appear to have the highest relative fitness. Ahn's study also demonstrated the existence of a standardized directional selection gradient for stature that is negative and relatively moderate, and standardized directional selection gradients for traits influencing thoracic volumes that are positive and higher. From these findings it was inferred, therefore, that there has been weak selection for shorter stature as well as strong selection for higher thoracic volume in this population. A further inference was that the traits of adaptive significance are still also liable to be influenced directly by environmental factors, such as hypoxia, that are inescapable at high altitude. In combination with the long-known distinctions in morphology between high and low altitude Andean populations, as well as our immediately previously documented pattern of heritability estimates in this population, Ahn's measurements of selection provided strong support for the hypothesis that directional evolutionary changes, in which genotype and phenotype are causally related, appear to have taken place in this human population long exposed to an extreme environment.

The analysis carried out by Melton (Chapter 8), comparing the core subset of the Tacna high to low altitude migrant data with observations on high altitude native Camacani residents, showed that the two groups of children sharing high altitude ancestry are both similar and different, with the resemblances as well as the distinctions being informative about the mediation of physical development patterns. While the Tacna group resident at low altitude is on average taller and heavier, these differences are mostly accounted for by stature, not by the distribution of adipose or other soft tissue. Particularly informative is the finding that the chest dimensions for Tacna males and females were overall at least as great as, or greater than, those of Puno males and females. Sternal length, one of the most noticeable traits of highlanders in the Andes, is significantly increased in Tacna children.

If hypoxia were proximately responsible for producing the developmental increase in chest size characteristic of Andean high altitude populations, the Tacna group resident at low altitude would be expected to show a reduction in chest size, as the first generation not exposed to hypoxic stress. In fact, the chest sizes of Tacna males are equal to or absolutely greater than those of males resident in Camacani, near the city of Puno, at high altitude. For females, the picture is less conclusive, but for most of the traits, Tacna females also have thoraxes at least as

large as those of the Puno females, and exceed them for transverse diameter, sternal length, and three other traits.

Reduced environmental stresses in the low-altitude population could have resulted in this group having greater overall body sizes during the growth period, but the environmental influences in themselves would not be expected to account for the expression of enlarged thoracic dimensions similar to those observed in Andean populations resident at high altitude. In the absence of direct exposure to the hypoxia theorized to be an important proximate influence on thoracic enlargement in high-altitude Andean populations, comparable thoracic enlargement among offspring born at low altitude to parents of high altitude ancestry clearly suggests the existence of a genetic influence on the growth patterns of these Andean people. Independently, then, Melton's results support the idea that major components of body proportions are under different genetic control mechanisms, and are consistent with the idea that genes influencing the relative growth of different morphological complexes are responsive to selective influences.

Lincoln (Chapter 4) made use of the battery of measurements included in the full list of the International Biological Program on subsamples of adult males from two groups that differed in ancestry (Quechua versus Aymara) but were resident in relatively comparable environmental settings along the shores of Lake Titicaca. Of 38 univariate comparisons between Camacani and the group sampled from Huata and Coata, 14 proved to be statistically significant (p < .05), with the Aymara having the larger mean value in 13 of the significant comparisons. Quite simply, the Coata and Huata Quechua resembled more closely the Nuñoa Quechua overall, establishing clearly that in proximate influences on numerous measures of body size and proportion (and even for specific shape features such as facial breadth) in these populations, ethnicity outweighed residence in more comparable ecological settings. Some degree of immediate environmental influence, quite possibly reflecting nutritional factors, also can be inferred from the observation that the Camacani Aymara were consistently taller, heavier, and fatter than either Quechua group. These findings make it worthwhile to reconsider the extent to which the Nuñoa Quechua have been considered as providing an appropriate general model for all high altitude Andean populations.

The study by Whittaker (Chapter 3) set out to examine the relationship of FVC and thoracic and overall body morphology to estimates of fat-free mass (defined as the difference between total body weight and the weight of all fat) in a sample of Aymara men born and raised at high altitude. Among the 20 anthropometric measurements included in the survey, height proved to be the best single predictor of FVC, with an R^2 of 0.40; this is a finding

similar to those of many studies performed on populations resident at sea level. However, when chest expansion was added to the model, the R^2 increased to 0.56. The best three-variable model contained the variables age, height, and chest expansion, yielding an R^2 of 0.62, whereas the addition of acromial height gave an R^2 of 0.64 and constituted the best four-variable model. The most parsimonious model was the three-variable model, and this was considered to be the best anthropometric model. When FFM was added, a four-variable model was created, but this gave no increase in R^2. Therefore, the null hypothesis (that addition of FFM as an independent variable does not significantly increase the accuracy of the model) could not be rejected. Overall, the results of this study tended to reinforce, once again, the inference that thoracic dimensions are key components of the functional and adaptive biological complex exhibited by high altitude Andean populations, to a much greater extent than is the case for lowlanders.

In all, the most straightforward explanation for all the outcomes reported here is that Andean populations resident at high altitude, with its unavoidable hypoxic stress, for ten or more millennia, have accumulated genes that are capable of producing enlarged thoracic dimensions relative to those of native lowland populations. Although further large-scale studies are needed, it appears that some of these genes are shared in common by Quechua and Aymara speakers, which represent populations that share some degree of common high altitude ancestry. The greater thoracic dimensions of Andean high altitude populations are related functionally to enhanced pulmonary functions such as forced vital capacity (FVC) that comprise part of the response to hypoxia. When, in addition to hypoxia, other stresses are present, such as cold and undernutrition, any enhanced thoracic development may come at the expense of overall body size as reflected in stature and weight. However, when populations of high altitude Andean ancestry migrate to low altitude environments characterized by reduced nutritional and cold stress, as well as an absence of hypoxia, stature and weight increase but not at the expense of thoracic dimensions.

Results presented here demonstrate that the characteristic thoracic form and body proportions of Andean highlanders have substantial heritable components that can be explained in terms of natural selection operating over the course of ten to twenty millennia in this extreme environment. As noted by Eckhardt (1985), we now have an example of skeletally-based morphological change in humans that not only is quantifiable, but can be shown to have occurred at rates even higher than those estimated for such classic examples as the expansion in brain size over the course of human evolution.

BIBLIOGRAPHY

Ahn, Y.I. 1986. Heritability measures of four anthropometric measurements on the thorax in a high altitude Peruvian population. M.S. thesis, The Pennsylvania State University, University Park, Pennsylvania.

Ahn, Y.I. 1990. Measurement of natural selection on correlated anthropometric characters in a high altitude Andean population. Ph.D. thesis, The Pennsylvania State University, University Park, Pennsylvania.

Ahn, Y.I. and R.B. Eckhardt. 1988. Genetic continuities and environmental contrasts: High altitude ancestry expressed at high and low altitudes. Am J Phys Anthro 75:179.

Allison, A.C. 1961. Genetic factors in resistance to malaria. Ann New York Acad Sci 91:710-729.

Antonovics, J., A.D. Bradshaw, and R.G. Turner. 1971. Heavy metal tolerance in plants. Adv Ecol Res 7:1-72.

Arnaud, J., N. Gutierrez, W. Tellez, and H. Vergnes. 1985. Haematology and erythrocyte metabolism in man at high altitude: An Aymara-Quechua comparison. Am J Phys Anthro 67:279-284.

Arnold, S.J. 1981. Behavioral variation in natural populations. I. Phenotypic, genetic and environmental correlations between chemoreceptive responses to prey in the garter snake, Thamnophis elegans. Evol 35:489-509.

Arnold, S.J. 1987. Quantitative genetics and selection in natural populations: Microevolution of vertebral numbers in the garter snake, Thamnophis elegans. IN: B. S. Weir, E. J. Eisen, M. M. Goodman, and G. Namkoong, eds., Proceedings of the Second International Conference on Quantitative Genetics. Sinauer Associates, Sunderland, Mass., pp. 619-636.

Arnold, S.J. and M.J. Wade. 1984a. On the measurement of natural and sexual selection: Theory. Evol 38:709-719.

Arnold, S.J. and M.J. Wade. 1984b. On the measurement of natural and sexual selection: Applications. Evol 38:720-734.

Askew, E.W. and A.L. Heckler. 1976. Adipose tissue cell size and lipolysis in the rat: Response to exercise intensity and food restriction. J Nutr 106:1351-1360.

Astrand, P.O. 1952. Experimental Studies of Physical Working Capacity in Relation to Sex and Age. Ejnar Munksgarrd, Copenhagen.

Bailey, J.K. and B. Weidman. 1990. Hearing and hypoxia among the Aymará. IN: W.J. Schull and F. Rothhammer, eds., The Aymara: Strategies in Adaptation to a Rigorous Environment. Kluwer Academic Publishers, Dordrecht, pp. 143-165.

Baker, P.T. (ed.). 1968. High Altitude Adaptation in a Peruvian Community. Occasional Papers in Anthropology, Number 1. Department of Anthropology, The Pennsylvania State University, University Park, Pennsylvania.

248

Baker, P.T. 1969. Human adaptation to high altitude. Science 163:1149-1156.

Baker, P.T. 1978. The adaptive fitness of high-altitude populations. IN: P.T. Baker, ed., The Biology of High-Altitude Peoples. Cambridge University Press, Cambridge, pp. 317-350.

Baker, P.T., E.E. Hunt, and S.T. Sen. 1958. The growth and interrelationships of skinfold and brachial tissue in man. Am J Phys Anthro 16:39-59.

Baker, P.T., and M.A. Little. 1976. Man in the Andes: A Multidisciplinary Study of High-Altitude Quechua. Dowden, Hutchison, and Ross, Stroudsburg, Pennsylvania.

Ballew, C. and J.D. Haas. 1986. Altitude differences in body composition among Bolivian newborns. Hum Biol 58:871-882.

Battaglia, B. 1958. Balanced polymorphism in Tisbe reticulata, a marine copepod. Evol 12:358-364.

Beall, C.M. 1980. Some aspects of the study of physical growth at high altitudes in Asia. IN: Environment and Human Population Problems at High Altitude, Seminaire, Centre National de la Recherche Scientifique, National Science Foundation, Paris, 1-3 October, 1980, pp. 49-54.

Beall, C. M. 1982. A comparison of chest morphology in high altitude Asian and Andean populations. Hum Biol 54:145-163.

Beall, C.M., P.T. Baker, T.S. Baker, and J.D. Haas. 1977. The effects of high altitude on adolescent growth in southern Peruvian Amerindians. Hum Biol 49:109-124.

Becker, W.A. 1964. Manual of Procedures in Quantitative Genetics. Washington State University Press, Pullman, Washington.

Behnke, A.R. 1953. The relation of lean body weight to metabolism and some consequent systematizations. Ann NY Acad Sci 56:1095-1142.

Bennett, W.C. 1946. The Andean highlands. IN: J.H. Steward, ed., Handbook of South American Indians, Vol. 2. Smithsonian Institution, Bureau of American Ethnology, Bull. #143, Washington, D.C., pp. 1-61.

Berry, R.J. and J.H. Crothers. 1968. Stabilising selection in the dog-whelk (Nucella lapillus). J Zool 155:5-17.

Berry, R.J., W.N. Bonner, and J. Peters. 1979. Natural selection in house mice (Mus musculus) from South Georgia (south Atlantic Ocean). J Zool 189:385-398.

Bishop, J.A., and L.M. Cook. 1981. Genetic Consequences of Man-Made Change. Academic Press, London.

Blackith, R.E. and R.A. Reyment. 1971. Multivariate Morphometrics. Academic Press, NY.

Boag, P.T. and P.R. Grant. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galapagos. Science 214:82-84.

Boas, F. 1912. Changes in the bodily form of descendents of immigrants. Am Anthro 14:530-563.

Bogin, B. 1988. Rural-to-urban migration. IN: C.G.N. Mascie-Taylor and G.W. Lasker, eds., Biological Aspects of Human Migration. Cambridge University Press, Cambridge, pp. 90-129.

Bogin, B. and R.B. McVean. 1981. Biosocial effects of urban migration on the development of families and children in Guatemala. Am J Pub Health 71:1373-1377.

Bonney, G.E. and R.C. Elston. 1985. Likelihood models for multivariate traits in human genetics. Biomet J 27:553-563.

Boorstein, W.R., N.C. Vamvakopoulos, and J.C. Fiddes. 1982. Human chorionic gonadotropin beta subunit is encoded by at least eight genes arranged in tandem and inverted pairs. Nature 300:419-422.

Boyce, A.J., J.S. Haight, D.B. Rimmer, and G.A. Harrison. 1974. Respiratory function in Peruvian Quechua Indians. Ann Hum Biol 1:137-148.

Brigada Tecnical de Campo. 1976. Comunidad campesina: "Camacani". Informe no. 76-BTC-AOR-ORAMS VIII, SINAMOS, Departamento del Puno, Peru.

Brodie, E.D. III. 1989. Genetic correlations between morphology and antipredator behaviour in natural populations of garter snake Thamnophis ordinoides. Nature 342:542-543.

Buechler, H.C. and J.M. Buechler. 1971. The Bolivian Aymara. Holt, Rinehart and Winston, NY.

Bumpus, H.C. 1899. The elimination of the unfit as illustrated by the introduced sparrow, Passer domesticus. Biological Lectures from the Marine Biological Laboratory. Woods Hole, Mass., pp. 209-228.

Burdette, W.J. 1963. Methodology in Mammalian Genetics. Holden-Day, San Francisco.

Burgert, S.L. and C.F. Anderson. 1979. An evaluation of upper arm measurements used in nutritional assessment. Am J Clin Nutr 32:2136-2142.

Burghardt, G.M. 1971. Chemical-cue preferences of newborn snakes: influence of prenatal maternal experience. Science 171:921-923.

Burt, C., and C. Banks. 1947. A factor analysis of body measurements for British adult males. Ann Eugen 13:238-256.

Butzer, K.W. 1971. Environment and Archaeology. Aldine, Chicago.

Cavalli-Sforza, L.L. and W.F. Bodmer. 1971. The Genetics of Human Populations. W. H. Freeman & Co., San Francisco.

Charlesworth, B. 1984. Some quantitative methods for studying evolutionary patterns in single characters. Paleobiology 10:308-318.

Cheverud, J.M. 1988. A comparison of genetic and phenotypic correlations. Evol 42:958-968.

Cheverud, J.M., J.J. Rutledge., and W.R. Atchley. 1983. Quantitative genetics of development: Genetic correlations among age-specific trait values and the evolution of ontogeny. Evol 37:895-905.

Clark, P.J. 1955. The heritability of certain anthropometric characters as ascertained from measurements of twins. Am J Hum Genet 8:49-54.

Clarke, C.A. and P.M. Sheppard. 1960. Supergenes and mimicry. Heredity 14:175-185.

Clegg, E.J., J.A. Harrison, and P.T. Baker. 1970. The impact of high altitude on human populations. Hum Biol 42:486-518.

Clegg, E.J., I.G. Pawson, E.H. Ashton, and R.M. Flinn. 1972. The growth of children at different altitudes in Ethiopia. Phil Trans Roy Soc London 264:403-437.

Clutton-Brock, T.H., F.E. Guinness, and S.D. Albon. 1982. Red Deer: Behavior and Ecology of Two Sexes. University of Chicago Press, Chicago.

Collazos, C., I. Moscoso, Y. Bravo, A. Castellanos, C. Caceres, A. Roca, and R. Bradfield. 1960. La alimentation y el estada de nutricion en el Peru. Annals de la Facultad de Medicina 43:7-297.

Collins, J.L. 1988. Unseasonal Migrations: The Effects of Rural Labor Scarcity in Peru. Princeton University Press, Princeton, New Jersey.

Consolazio, C.F., R.E. Johnson, and L.J. Pecora. 1963. Physiological Measurements of Metabolic Function in Man. McGraw-Hill, NY.

Consolazio, C.F., L.O. Matoush, H.L. Johnson, and T.A. Daws. 1968. Protein and water balances of young adults during prolonged exposure to high altitude. Am J Clin Nutr 21:154-161.

Cornfield, J. 1962. Joint dependence of risk of coronary heart disease on serum cholesterol and systolic blood pressure: A discriminant function analysis. Fed Proc 21:58-61.

Cotlear, D., H. Martinez, J. Leon, and J. Portugal. 1987. Peru: la Poblacian Migrante. Asociacione Multidisciplinaria de Investigacion y Docencia in Poblacion, Lima, Peru.

Cowgill, G.R. 1957. A formula for estimating the specific gravity of the human body with a consideration of its possible uses. Am J Clin Nutr 5:601-611.

Crow, J.F. 1958. Some possibilities for measuring selection intensities in man. Hum Biol 30:1-13.

Cruz-Coke, R. 1978. A genetic description of high-altitude populations. IN: P.T. Baker, ed., The Biology of High-Altitude Peoples. Cambridge University Press, Cambridge, pp. 47-64.

Cruz-Coke, R., A.P. Cristoffanini, M. Aspillaga, and F. Biancani. 1966. Evolutionary forces in human populations in an environmental gradient in Arica, Chile. Hum Biol 38:421-432.

Darwin, C. 1859. On the Origin of Species by Means of Natural Selection. Murray, London.

DeJong, G.F., and R.W. Gardner, eds. 1981. Migration Decision Making. Pergamon Press, NY.

Devi, M.R. and G.G. Reddi. 1983. Heritability of body measurements among the Jalari population in Visakhapatnam. Ann Hum Biol 10:483-485.

Dobzhansky, Th. 1970. Genetics of the Evolutionary Process. Columbia University Press, NY.

Donayre, J. 1966. Population growth and fertility at high altitude. IN: A. Hurtado, ed., Life at High Altitudes. Pan-American Health Organization, Washington, D.C., pp. 140-160.

Dowdeswell, W.H. 1961. Experimental studies on natural selection in the butterfly Maniola jurtina. Heredity 16:39-52.

Dubos, R. 1965. Man Adapting. Yale University Press, New Haven.

Dutt, J.S. 1976. Population movement and gene flow. IN: P.T. Baker and M.A. Little, eds., Man in the Andes: A Multidisciplinary Study of High-Altitude Quechua. Dowden, Hutchinson, and Ross, Stroudsburg, Pennsylvania, pp. 98-114.

Eckhardt, R.B. 1985. Rapid morphometric change in human skeletal traits: an example from the Andean Highlands. IN: P.V. Tobias, ed., Hominid Evolution: Past, Present and Future. Alan R. Liss, Inc., NY, pp. 256-288.

Eckhardt, R.B. and J.S. Dutt. 1979. Growth and development of the chest in Aymara Indians living at high altitude in Southern Peru (abstract). Am J Phys Anthro 50:435-444.

Eckhardt, R.B., and A.A. Kramer. 1980. Thoracic form in high altitude Andean natives: Mosaic morphological patterning documented by standard and non-standard anthropometric measurements (abstract). Am J Phys Anthro 53:223.

Eckhardt, R.B., A.A. Kramer, and J.S. Dutt. 1981. Genetic and environmental influences on thoracic morphology in high altitude Andean natives. Am J Phys Anthro 54:216.

Eckhardt, R.B., M.H. Flores, and D.A. Eckhardt. 1982. A three way population comparison partitions genetic and environmental influences on thoracic morphology and body size in high altitude Andean natives (abstract). Am J Phys Anthro 57:184.

Eckhardt, R.B., C.D. Eckhardt, and M.H. Flores. 1983. Genetic and environmental influences on growth and development in Aymara and Quechua populations native to high altitude in southern Peru (abstract). Am J Phys Anthro 60:191.

Eidt, R.C. 1968. The climatology of South America. IN: E.J. Fittkau, ed., Biogeography and Ecology of South America. Dr. W. Junk Publishers, The Hague, pp. 1-56.

Endler, J.A. 1986. Natural Selection in the Wild. Princeton University Press, Princeton.

Erickson, E.E., W. Barnes, F.H. Chaffee, G. DeCicco, S.G. Fortenbaugh, S.J. Lehmann, S. Malik. 1965. U.S. Army Area Handbook for Peru. U.S. Government Printing Office, Washington, D.C.

Falconer, D.S. 1960. Introduction to Quantitative Genetics. Oliver and Boyd, Edinburgh.

Falconer, D.S. 1963. Quantitative inheritance. IN: W.J. Burdette, ed., Methodology in Mammalian Genetics. Holden-Day, San Francisco, pp. 193-216.

Falconer, D.S. 1972. Introduction to Quantitative Genetics. The Ronald Press Co., NY.

Falconer, D.S. 1981. Introduction to Quantitative Genetics. Longman Scientific & Technical, London.

Falconer, D.S. 1983. Introduction to Quantitative Genetics. Longman Scientific & Technical, NY.

Falconer, D.S. 1989. Introduction to Quantitative Genetics. Longman Scientific & Technical, Essex, England.

Fisher, R.A. 1930. The Genetical Theory of Natural Selection. Oxford University Press, Oxford.

Forbes, D. 1870. On the Aymara indians of Bolivia and Peru. J Ethnol Soc Lond II(XXIII):193-305.

Ford, E.B. 1975. Ecological Genetics. Chapman and Hall, London.

Frisancho, A.R. 1969. Human growth and pulmonary function of a high altitude Peruvian Quechua population. Hum Biol 41:365-379.

Frisancho, A.R. 1975. Functional adaptation to high altitude hypoxia. Science 187:313-319.

Frisancho, A.R. 1976. Growth and morphology at high altitude. IN: P.T. Baker and M.A. Little, eds., Man in the Andes: A Multidisciplinary Study of High-Altitude Quechua. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, pp. 180-207.

Frisancho, A.R. 1978. Human growth and development among high-altitude populations. IN: P.T. Baker, ed., The Biology of High-Altitude Peoples. Cambridge University Press, Cambridge, pp. 117-172.

Frisancho, A.R. 1981. Human Adaptation: A Functional Interpretation. University of Michigan Press, Ann Arbor.

Frisancho, A.R. and P.T. Baker. 1970. Altitude and growth: A study of the patterns of physical growth of a high altitude Peruvian Quechua population. Am J Phys Anthro 32:279-292.

Frisancho, A.R., S.M. Garn, and W. Ascoli. 1970. Childhood retardation resulting in reduction of adult body size due to lesser adolescent skeletal delay. Am J Phys Anthro 33:325-336.

Frisancho, A.R., T. Velasquez, and J. Sanchez. 1973. Influence of developmental adaptation on lung function at high altitude. Hum Biol 45:583-594.

Frisancho, A.R., G.A. Borkan, and J.E. Klayman. 1975. Pattern of growth of lowland and highland Peruvian Quechua of similar genetic composition. Hum Biol 47:233-243.

Garruto, R.M. 1969. Pulmonary function and body morphology: selected relationships studied at high altitude. M.A. thesis, Department of Anthropology, The Pennsylvania State University, University Park, Pennsylvania.

Garruto, R.M. and C.J. Hoff. 1976. Genetic history and affinities. IN: P.T. Baker and M.A. Little, eds., Man in the Andes: A Multidisciplinary Study of High Altitude Quechua. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, pp. 98-114.

Gnanadesikan, R. 1977. Methods for Statistical Data Analysis of Multivariate Observations. John Wiley & Sons, NY.

Goddard, R.F., B. Balke, and U.C. Luft. 1967. The Effect of Altitude on Physical Perfomance. The Athletic Institute, Chicago.

Goldstein, H. 1986. Sampling for growth studies. IN: F. Falkner and J.M. Tanner, eds., Human Growth, A Comprehensive Treatise. Plenum Press, NY, pp. 183-208.

Goldstein, M.S. 1943. Demographic and Bodily Changes in Descendants of Mexican Immigrants. Institute of Latin American Studies, The University of Texas, Austin, Texas.

Goodnight, C.J. 1988. Epistasis and the effect of founder events on the additive genetic variance. Evol 42:441-454.

Greksa, L.P. 1986. Chest morphology of young Bolivian high-altitude residents of European ancestry. Hum Biol 58:427-443.

Greksa, L.P., H. Spielvogel, M. Paz-Zamora, E. Caceres, and L. Paredes-Fernandez. 1988. Effect of altitude on the lung function of high altitude residents of European ancestry. Am I Phys Anthro 75:77-85.

Greulich, W.W. and S.I. Pyle. 1959. Radiographic Atlas of Skeletal Development of the Hand and Wrist. Stanford University Press, Stanford.

Groeters, F.R. 1988. Relationship between observed components of variance and causal components of variance in a split-family, half-sib, full-sib analysis. Evol 42:631-633.

Guerra-Garcia, R. 1971. Testosterone metabolism in men exposed to high altitudes. Acta Endocrin Panama 2:55-62.

Gursky, M. 1969. A dietary survey of three Peruvian highland communities. M.A. thesis, The Department of Anthropology, The Pennsylvania State University, University Park, Pennsylvania.

Haas, J.D., E.A. Frongillo, C.D. Stepdick, J.L. Beard, and A. Hurtado. 1980. Altitude, ethnic and sex differences in birth weight and length in Bolivia. Hum Biol 52:459-477.

Hager, A., L. Sjostrom, B. Arvidsson, P. Bjorntorp, and U. Smith. 1976. Body fat and adipose tissue cellularity in infants: A longitudinal study. Metabol Clin Exper 26:607-614.

Haldane, J.B.S. 1949. Disease and evolution. Ricerca Scient. Suppl. 19:68-76.

Haldane, J.B.S. 1954. The measurement of natural selection. Proc IX Internat Cong Gen 1:480-487.

Hammond, W.H. 1957. The constancy of physical types as determined by factor analysis. Hum Biol 29:40-61.

Harrison, G.A., J.S. Weiner, J.M. Tanner, and N.A. Barnicot. 1977. Human Biology: An Introduction to Human Evolution, Variation, Growth and Ecology. Oxford University Press, Oxford.

Hartl, D.L. and A.G. Clark. 1989. Principles of Population Genetics. Sinauer Associates, Sunderland, Mass.

Heath, D. and D.R. Williams. 1977. Man at High Altitude. Churchill Livingstone, NY.

Hecht, M.K. 1952. Natural selection in the lizard genus Aristelliger. Evol 6:112-124.

Hendrickson, A.E. and P.O. White. 1964. Promax: A quick method for rotation to oblique simple structure. Brit J Math and Stat Psych 17:65-70.

Hepper, N.G., W.S. Fowler, and H.F. Helmholz. 1960. Relationship of height to lung volume in healthy men. Diseases Chest 37:314-320.

Hewitt, D. 1957. Some familial correlations in height, weight, and skeletal maturity. Hum Genet 22:26-35.

Hill, W.G. 1978. Estimation of heritability by regression using collateral relatives: linear heritability estimation. Gen Res 32:265-274.

Hill, W.G. and R. Thompson. 1978. Probabilities of non-positive definite between-group or genetic covariance matrices. Biometrics 34:429-439.

Hiorns, R.W. and G.A. Harrison. 1970. Sampling for the detection of natural selection by age group differences. Hum Biol 42:53-64.

Hoff, C.J. 1972. Preliminary observations on altitudinal variation in the physical growth and development of Peruvian Quechua. Ph.D. thesis, The Pennsylvania State University, University Park, Pennsylvania.

Hoff, C.J. 1974. Altitudinal variations in the physical growth and development of Peruvian Quechua. Homo 24:87-99.

Howells, W.W. 1951. Factors of human physique. Am J Phys Anthro 9:159-192.

Howells, W.W. 1957. Variation of External Body Form in the Individual. Peabody Museum of Harvard University, Cambridge, Mass.

Hurtado, A. 1932a. Respiratory adaptation in the Indian natives of the Peruvian Andes: Studies at high altitude. Am J Phys Anthro 17:137-165.

Hurtado, A. 1932b. Studies at high altitude: Blood observations on the Indian natives of the Peruvian Andes. Am J Phys Anthro 18:487-505.

Hurtado, A. 1971. The influence of high altitude on physiology. IN: R. Porter and J. Knight, eds., High Altitude Physiology: Cardiac and Respiratory Aspects. Churchill Livingstone, London, pp. 1-43.

Hussein, F.H., I. Ghaly, A. Aly, and S. Shoukry. 1984. Age at menarche in Egyptians. IN: J. Borms, R. Hauspie, A. Sand, C. Susanne, and M. Hebbelinck, eds., Human Growth and Development. Plenum Press, NY, pp. 431-436.

Illsley, R., A. Finlayson, and B. Thompson. 1963. The motivation and characteristics of internal migrants: a socio-medical study of young migrants in Scotland. Milbank Memorial Fund Quarterly 41:115-144.

Jenks, W.F. 1956. Peru. IN: W.F. Jenks, ed., Handbook of South American Geology. Geological Society of America, NY.

Johnson, R.A. and D.W. Wichern. 1982. Applied Multivariate Statistical Analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

Johnston, R.F., D.M. Niles, and S.A. Rohwer. 1972. Hermon Bumpus and natural selection in the house sparrow Passer domesticus. Evol 26:20-31.

Kalnina, O.V., F. Saratsetseg, V.V. Kalnin, and Yu.P. Altukhov. 1988. Correlation between variability of polygenic morphological and monogenic biochemical characters in Karakul sheep. Sov Gen 24:99-106.

Kaplan, B. 1954. Environment and human plasticity. Am Anthro 56:780-799.

Karn, M.N. and L.S. Penrose. 1951. Birth weight and gestation time in relation to maternal age, parity, and infant survival. Ann Eug 16:147-164.

Kempthorne, O. and O.B. Tandon. 1953. The estimation of heritability by regression of offspring. Biometrics 9:90-100.

Kendall, M.G. and A. Stuart. 1961. The Advanced Theory of Statistics, Vol. 3. Charles Griffin and Co., London.

Kendall, M.G. and A. Stuart. 1979. The Advanced Theory of Statistics, Vol 2. Macmillan Publishing Co., NY.

Kettlewell, H.B.D. 1973. The Evolution of Melanism. Clarendon Press, Oxford.

Kin, J. and C.W. Mueller. 1978. Introduction to Factor Analysis. Sage Publications, London.

Klecka, W.R. 1980. Discriminant Analysis. Sage Publications, London.

Klissouras, V. 1984. Factors affecting physical performance with reference to heredity. IN: J. Borms, R. Hauspie, A. Sand, C. Susanne, and M. Hebbelinck, eds., Human Growth and Development. Plenum Press, NY, pp. 453-470.

Kohn, L.A. and Atchley, W.R. 1988. How similar are genetic correlation structures?: Data from mice and rats. Evol 42:467-481.

Kouchi, M. 1979. On the validity of principal component analysis as a method of analysis of the variations in human physique. I. Selection of the measurement items based on the first three principal components. J Anthro Soc Nippon 87:423-438.

Kramer, A.A. 1980. Heritability estimates of thoracic skeletal dimensions for a high-altitude Peruvian population. M.S. thesis, The Pennsylvania State University, University Park, Pennsylvania.

La Barre, W. 1948. The Aymara Indians of the Lake Titicaca Plateau, Bolivia. Am Anthro 50:1-250.

Lahiri, S., R.G. Delaney, J.S. Brody, M. Simpser, T. Velasquez, E.K. Motoyama, and C. Polgar. 1976. Relative role of environmental and genetic factors in respiratory adaptation to high altitude. Nature 261:132-134.

La Lone, D.E. 1985. Andean ethnohistory: Words of scholars on the works of conquerors. Rev Anthro 12:41-48.

Landauer, C.A. 1962. A factor analysis of the facial skeleton. Hum Biol 34:239-253.

Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. Evol 33:402-416.

Lande, R. 1980a. Genetic variation and phenotypic evolution during allopatric speciation. Am Nat 116:463-479.

Lande, R. 1980b. The genetic covariance between characters maintained by pleiotropic mutations. Genetics 94:203-215.

Lande, R. 1982. A quantitative genetic theory of life history evolution. Ecology 62:607-615.

Lande, R. 1985. Genetic and evolutionary aspects of allometry. IN: W. L. Jungers, ed., Size and Scaling in Primate Biology. Plenum Publishing Co., NY, pp. 21-32.

Lande, R. and Arnold, S.J. 1983. The measurement of selection on correlated characters. Evol 37:1210-1226.

Lasker, G.W. 1946. Migration and physical differentiation. Am J Phys Anthro 4:273-300.

Leamy, L. 1974. Heritability of osteometric traits in a randombred population of house mice. J Hered 65:109-120.

Leamy, L. 1976. Genetic and environmental correlations of morphometric traits in randombred house mice. Evol 31:357-369.

Lederberg, J. 1969. Health in the world of tomorrow. IN: Third PAHO/WHO Lecture on the Biomedical Sciences. Pan-American Health Organization, Washington, D.C.

Leonard, W.R. 1989. Nutritional determinants of high-altitude growth in Nuñoa, Peru. Am J Phys Anthro 80:341-352.

Leonard, W.R. and R.B. Thomas. 1989. Biosocial responses to seasonal food stress in highland Peru. Hum Biol 61:65-85.

Lerner, I.M. and C.A. Gunns. 1952. Egg size and reproductive fitness. Poult Sci 31:537-544.

Lincoln, D.S. and R.B. Eckhardt. 1984. Multivariate analysis of metric traits in the Amerindians living at high altitude in southern Peru (abstract). Am J Phys Anthro 63:185.

Livingstone, F.B. 1969. Polygenic models for the evolution of human skin color difference. Hum Biol 41:480-493.

Llerena, L.A. 1973. Determination of luteinizing hormone with radioimmunoassay: Physiological variations and the effects of altitude. Dissertation, Institute for Investigations in Altitude, Lima, Peru.

Lofsvold, D. 1986. Quantitative genetics of morphological differentiation in Peromyscus. I. Tests of the homogeneity of genetic covariance structure among species and subspecies. Evol 40:559-573.

Lohman, T.G. 1981. Skinfolds and body density and their relation to body function: A review. Hum Biol 53:181-226.

Lynch, T.F. and K.A.R. Kennedy. 1970. Early human cultural and skeletal remains from Guitarrero Cave, Northern Peru. Science 169:1307-1309.

MacNeish, R.S. 1971. Early man in the Andes. Sci Am 224:36-41.

MacNeish, R.S., R.S. Berger, and R. Protsch. 1970. Megafauna and man from Ayacucho, highland Peru. Science 168:975-977.

Maletta, H. and A. Bardeles. 1985. Peru: las provincias en cifras 1876-1981. Universidad del Pacifico, Lima, Peru.

Malhotra, M.S. 1966. People of India including primitive tribes: A survey of physiological adaptation, physical fitness, and nutrition. IN: P.T. Baker and J.S. Wiener, eds., The Biology of Human Adaptability. Clarendon Press, Oxford, pp. 329-356.

Malik, S.L. and J.P. Singh. 1979. Lung function in Highlander Bods of Ladakh. Am J Phys Anthro 51:383-388.

Malina R.M. 1969. Quantification of fat, muscle, and bone in man. Clin Ortho 65:9-38.

Malina, R.M. 1980. The measurement of body composition. IN: F.E. Johnston, A.F. Roche, and C. Susanne, eds., Physical Growth and Maturation. Plenum Press, NY, pp. 35-60.

258

Malina, R.M., J.H. Himes, C.D. Stepick, F.G. Lopez and P.H. Bushang. 1981. Growth of rural and urban children in the Valley of Oaxaca, Mexico. Am J Phys Anthro 55:269-280.

Malmberg, G. 1988. Metropolitan Growth and Migration in Peru. University of Umea, Umea, Sweden.

Manly, B.F.J. 1975. The measurement of the characteristics of natural selection. Theor Pop Biol 7:288-305.

Manly, B.F.J. 1976. Some examples of double exponential fitness functions. Heredity 36:229-234.

Manly, B.F.J. 1977. A new index for the intensity of natural selection. Heredity 38:321-328.

Manly, B.F.J. 1985. The Statistics of Natural Selection on Animal Populations. Chapman and Hall, NY.

Martin, W.J. 1949. The Physique of Young Adult Males. Medical Research Council Memorandum 20. HMSO, London.

Masuda, T. 1965. Application of prinicipal component analysis and factor analysis to the measurements of the human body: A trial for designing ready-made garments. Rep Stat Appl Res 12:30-48.

Mather, K. and Jinks, J.L. 1982. Biometrical Genetics. Chapman and Hall, NY.

Mathews, D.K. and E.L. Fox. 1976. The Physiological Basis of Physical Education and Athletics. Saunders College Publishing, Philadelphia.

Mazess, R.B. 1975. Human adaptation to high altitude. IN: A. Damon, ed., Physiological Anthropology. Oxford University Press, NY, pp. 167-209.

Mazess, R.B. and P.T. Baker. 1964. Diet of Quechua Indians living at high altitude: Nuñoa, Peru. Am J Clin Nutr 15:341-351.

McCloy, E.H. 1940. An analysis for multiple factors of physical growth at different age levels. Child Dev 11:249-277.

McFarlane, J. 1990. Ecologic determinants of the health of Aymara children. IN: W.J. Schull and F. Rothhammer, eds., The Aymara. Kluwer Academic Publishers, London, pp. 87-100.

McGregor, P.K., J.R. Krebs, and C.M. Perrins. 1981. Song repertoires and lifetime reproductive success in the great tit (Parus major). Am Nat 118:149-159.

Mednick, B.R., K.M. Finello, R.L. Baker, and S.A. Mednick. 1984. Psychosocial aspects of growth. IN: J. Borms, R. Hauspie, A. Sand, C. Susanne, and M. Hebbelinck, eds., Human Growth and Development. Plenum Press, NY, pp. 657-674.

Meggers, B.J. 1972. Prehistoric America. Aldine-Atherton, Chicago.

Merino, C. and C. Reynafarje. 1949. Bone marrow studies in polycythemia of high altitudes. J Lab Clin Med 34:637-649.

Mitchell-Olds, T. and J.J. Rutledge. 1986. Quantitative genetics in natural populations: A review of the theory. Am Nat 127:379-402.

Mitchell-Olds, T. and R.G. Shaw. 1987. Regression analysis of natural selection: Statistical inference and biological interpretation. Evol 41:1149-1161.

Mongé, M.C. and C.C. Mongé. 1966. High Altitude Diseases. Charles C. Thomas, Springfield.

Moore, L.G. and J.G. Regensteiner. 1983. Adaptation to high altitude. Ann Rev Anthro 12:285-304.

Mueller, W.H. 1975. Parent-child and sibling correlations and heritability of body measurements in a rural Colombian population. Ph.D. thesis, Department of Anthropology, The University of Texas, Austin.

Mueller, W.H., V.N. Schull, W.J. Schull, P. Soto, and F. Rothhammer. 1978a. A multinational Andean genetic and health program: Growth and development in an hypoxic environment. Ann Hum Biol 5:329-352.

Mueller, W.H., F. Yen, F. Rothhammer, and W.J. Schull. 1978b. A multinational Andean genetic and health program. VI. Physiological measurements of lung function in an hypoxic environment. Hum Biol 50:489-513.

Mueller, W.H., F. Yen, F. Rothhammer, and W.J. Schull. 1978c. A multinational Andean genetic and health program. VII. Lung function and physical growth-- multivariate analyses in high- and low-altitude populations. Aviation, Space and Environ Med 49:1188-1196.

Mueller, W.H., F. Murillo, H. Palamino, M. Badzioch, R. Chakrabory, P. Fuerst, and W.J. Schull. 1980. The Aymara of Western Bolivia. V. Growth and development in an hypoxic environment. Hum Biol 52:529-546.

Naeye, R.L. 1966. Organ and cellular development in mice growing at simulated high altitude. Lab Invest 15:700-706.

Naeye, R.L., M.W. Diener, H.T. Harcke, and W.A. Blanc. 1971. Relation of poverty and race to birthweight and organ cell structure in the newborn. Pediat Res 5:17-22.

Nance, W.E., L.A. Corey, and J.A. Boughman. 1978. Monozygotic twin kinships: A new design for genetic and epidemiological research. IN: N.E. Morton and C.S. Chung, eds., Genetic Epidemiology. Academic Press, NY, pp. 163-187.

Neter, J. and W.H. Wasserman. 1974. Applied Linear Statistical Models. Richard D. Irwin, Homewood, Illinois.

Neter, J., W. Wasserman, and M.H. Kutner. 1985. Applied Linear Statistical Models. Richard D. Irwin, Homewood, Illinois.

Newman, M. 1975. Nutritional adaptation in man. IN: A. Damon, ed., Physiological Anthropology. Oxford University Press, London, pp. 210-259.

Newman, R.W. and E.H. Munro. 1955. The relation of climate and body size in U.S. males. Am J Phys Anthro 13:1-17.

O'Donald, P. 1968. Measuring the intensity of natural selection. Nature 220:197-198.

O'Donald, P. 1970. Change of fitness by selection for a quantitative character. Theor Pop Biol 1:219-232.

O'Donald, P. 1971. Natural selection for quantitative characters. Heredity 27:137-153.

O'Donald, P. 1973. A further analysis of Bumpus' data: the intensity of natural selection. Evol 27:398-404.

Orlove, B.S. 1987. Mountain anthropology and mountain anthropologists: The comparative study of populations at high elevations. Rev Anthro 14:95-100.

Oscai, L.B., C. Spirakis, J.A. McGarr, and S.P. Bairak. 1974. Effect of exercise on adipose tissue cellularity. Fed Proc 33:1956-1958.

Palomino, H., W.H. Mueller, and W.J. Schull. 1979. Altitude, heredity, and body proportions in Northern Chile. Am J Phys Anthro 50:39-50.

Parizkova, J. 1963. Impact of age, diet, and exercise on man's body composition. Ann NY Acad Sci 110:661-674.

Parizkova, J. 1973. Body composition and exercise during growth and development. IN: G.L. Rarick, ed., Physical Activity: Human Growth and Development. Academic Press, NY, pp 98-124.

Pearson, K. 1903. Mathematical contributions to the theory of evolution. XI. On the influence of natural selection on the variability and correlation of organs. Phil Trans Roy Soc London Series A 200:1-66.

Pearson, O.P. 1951. Mammals in the highlands of southern Peru. Bull Mus Compar Zool 106:115-171.

Peñaloza, J.B. 1971. Crecimiento y desarrollo sexual del adolescente andino. Ph.D. thesis, Universidad Nacional Mayor de San Marcos, Lima, Peru.

Picón-Reátegui, E. 1976. Nutrition. IN: P.T. Baker and M.A. Little, eds., Man in the Andes: A Multidisciplinary Study of High-Altitude Quechua. Dowden, Hutchinson, and Ross, Stroudsburg, Pennsylvania, pp. 208-236.

Picón-Reátegui, E. 1978. The food and nutrition of high-altitude populations. IN: P.T. Baker, ed., The Biology of High-Altitude Peoples. Cambridge University Press, Cambridge, pp. 219-250.

Picón-Reátegui, E., R. Lozano, and J. Valdivieso. 1961. Body composition at sea levels and high altitudes. J Appl Phys 16:589-592.

Pierce, J. and T. Parsons. 1981. Glycoprotein hormones: structure and function. Ann Rev Biochem 50:465-495.

Prader, A. 1984. Biomedical and endocrinological aspects of normal growth and development. IN: J. Borms, R. Hauspie, A. Sand, C. Susanne, and M. Hebbelinck, eds., Human Growth and Development. Plenum Press, NY, pp. 1-22.

Preto, J.C. and M. Calderon. 1947. Estudios bioanthropometricos en los escolares Peruanos. Boletin del Instituto Psicopedagico Nationale, Lima, Peru.

Reeve, E.C.R. 1955. The variance of the genetic correlation coefficient. Biometrics 11:357-374.

Relethford, J.H., F.C. Lees, and P.J. Byard. 1978. The use of principal components in the analysis of cross-sectional growth data. Hum Biol 50:461-475.

Rendel, J.M. 1943. Variations in the weights of hatched and unhatched ducks' eggs. Biometrika 33:48-58.

Reynafarje, C., J. Faura, and V. Pimentel. 1965. El factor Diego y otros grupos sanguineos en los Indios de la sierra y selva peruana. Arch Inst Biol Andina 1:14-22.

Richardson, A.M.M. 1974. Differential climatic selection in natural populations of the land snail Cepaea nemoralis. Nature 247:572-573.

Riesenfeld, A. 1973. The effect of extreme temperatures and starvation on the body proportions of the rat. Am J Phys Anthro 39:427-460.

Roberts, D.F. 1953. Body weight, race, and climate. Am J Phys Anthro 11:533-538.

Roberts, D.F., W.Z. Billewicz, and I. MacGregor. 1978. Heritability of stature in a west African population. Ann Hum Genet 42:15-24.

Rogers, A. 1984. The effects of illness on growth during childhood and adolescence. M. Phil. thesis, Oxford University, Oxford, England.

Rony, H.R. 1940. Obesity and Leanness. Lea, Philadelphia.

Rothhammer, F. and R.S. Spielman. 1972. Anthropometric variation in the Aymara: Genetic, geographic and topographic contributions. Am J Hum Gen 24:371-380.

SAS User's Guide: Statistics. 1982. SAS Institute, Inc., Cary, North Carolina.

SAS User's Guide. 1979. SAS Institute, Inc., Cary, North Carolina.

Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. Evol 42:849-861.

Schmitt, L.H., G.A. Harrison, and R.W. Hiorns. 1988. Genetic and morphometric variances in three human populations. Ann Hum Genet 52:145-149.

Schreider, E. 1964. Ecological rules, body heat regulation, and human evolution. Evol 18:1-9.

Schull, W.J. and F. Rothhammer (eds.). 1990. The Aymara: Strategies in Adaptation to a Rigorous Environment. Kluwer Academic Publishers, Dordrecht.

Schull, W.J., B. Razmilíc, L. Figueroa, and M. González. 1990. Trace metals. IN: W.J. Schull and F. Rothhammer, eds. The Aymara: Strategies in Adaptation to a Rigorous Environment. Kluwer Academic Publishers, Dordrecht.

Schwabe, G.H. 1968. Towards an ecological characterization of the South American continent. IN: E.J. Fittkau, ed., Biogeography and Ecology of South America. Dr. W. Junk Publishers, The Hague, pp. 133-156.

Sciulli, P.W., C. Janini, and M. Giesen. 1988. Phenotypic selection on the dentition in a late archaic population of Ohio. Am J PhysAnthro 76:527-533.

Service, P.M. and M.R. Rose. 1985. Genetic covariation among life-history components: The effect of novel environments. Evol 39:943-945.

Severinghaus, J.W., C.R. Bainton, and A. Carcelen. 1966. Respiratory insensitivity to hypoxia in chronically hypoxic man. Respir Physiol 1:308-334.

Shapiro, H.L. 1939. Migration and Environment. Oxford University Press, NY.

Siri, W.E. 1961. Body composition from fluid spaces and density: Analysis of methods. IN: Techniques for Measuring Body Composition. National Academy of Science, National Research Council, Washington, D.C., pp. 22-34.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. W. H. Freeman, San Francisco.

Steegman, A.T. 1975. Human adaptation to cold. IN: A. Damon, ed., Physiological Anthropology. Oxford University Press, NY, pp. 130-166.

Steegman, A.T. 1985. 18th century British military stature: Growth cessation, selective recruiting, secular trends, nutrition at birth, cold and occupation. Hum Biol 57:77-95.

Steward, J. and L. Faron. 1959. Native Peoples of South America. McGraw-Hill, NY.

Stini, W.A. 1971. Evolutionary implications of changing nutritional patterns in human evolution. Am Anthro 73:1019-1030.

Stini, W.A. 1972. Malnutrition, body size, and proportion. Ecol Food Nutri 1:121-126.

Stinson, S. 1980. The physical growth of high altitude Bolivian Aymara children. Am J Phys Anthro 52:377-385.

Stinson, S. and A.R. Frisancho. 1978. Body proportions of highland and lowland Peruvian Quechua children. Hum Biol 50:57-68.

Stoudt, H.W., A. Damon, and R.A. McFarland. 1960. Heights and weights of white Americans. Hum Biol 28:111-123.

Stunkard, A. 1968. Environment and obesity: Recent advances in our understanding of regulation of food intake in man. Fed Proc 27:1367-1373.

Susanne, C. 1969. Genetics and environmental influence on morphological characteristics. Ann Hum Biol 2:279-287.

Susanne, C. 1977. Heritability of anthropological characters. Hum Biol 49:573-580.

Talmadge, K., W. Boorstein, and J.C. Fiddes. 1983. The human genome contains seven genes for the beta subunit of chorionic gonadotropin but only one gene for the beta subunit of luteinizing hormone. DNA 2:281-289.

Tanner, J.M. 1986. Growth as a target-seeking function. IN: F. Falkner and J.M. Tanner, eds., Human Growth, a Comprehensive Treatise. Plenum Press, NY, pp. 167-180.

Thomas, R.B. 1976. Energy flow at high altitude. IN: P.T. Baker and M.A. Little, eds., Man in the Andes: A Multidisciplinary Study of High-Altitude Quechua. Dowden, Hutchinson, and Ross, Stroudsburg, Pennsylvania, pp. 379-404.

Thomas, R.B. and B.P. Winterhalder. 1976. Physical and biotic environment of southern highland Peru. IN: P.T. Baker and M.A. Little, eds., Man in the Andes: A Multidisciplinary Study of High-Altitude Quechua. Dowden, Hutchinson, and Ross, Stroudsburg, Pennsylvania, pp. 21-59.

Thompson, R. 1977. The estimation of heritability with unbalanced data: I. Observation available on parents and offspring. Biometrics 33:485-495.

Thompson, J.M., Jr. and J.M. Thoday. 1979. Quantitative Genetic Variation. Academic Press, NY.

Turelli, M. 1988. Phenotypic evolution, constant covariance, and the maintenance of additive variance. Evol 42:1342-1347.

Ulizzi, L., R. Correani, and L. Terrenato. 1988. Effects of environmental changes on the phenotypic expression of human polygenic traits. Ann Hum Genet 52:341-349.

Vandemark, G.J. 1985. Heritability estimates of six anthropometric indicators of nutritional status in a high-altitude Peruvian population. M.S. thesis, The Pennsylvania State University, University Park, Pennsylvania.

Vandemark, G.J., C.M. Kelly, and R.B. Eckhardt. 1985. A PASCAL program which calculates heritability estimates using weighted linear regressions. J Hered 76:400-401.

Vandenberg, S.G. 1968. A factor analysis of garment measures of Dutch women. Hum Biol 40:295-313.

Van Valen, L. 1973. A new evolutionary law. Evol Theor 1:1-30.

Velasquez, T. 1976. Pulmonary function and oxygen transport. IN: P.T. Baker and M.A. Little, eds., Man in the Andes: A Multidisciplinary Study of High-Altitude Quechua. Dowden, Hutchinson, and Ross, Stroudsburg, Pennsylvania, pp. 237-260.

Vellard, J.A. 1976. Etude anthropometrique des populations indigenes du Perou et de la Bolivie. IN: Anthropologie des Populations Andines. Colloque INSERM 63:57-63.

Walker, P.L. 1983. An evaluation of genetic and environmental influence on skeletal morphology. Am J Phys Anthro 60:267.

Wallace, B. 1981. Basic Population Genetics. Columbia University Press, NY.

Weiner, J.S. and J.A. Lourie. 1969. Human Biology: A Guide to Field Methods. Blackwell Scientific, Oxford.

Weldon, W.F.R. 1901. A first study of natural selection in Clausilia laminata (Montagu). Biometrika 1:109-124.

Womersley, J. and J.V.G.A. Durnin. 1977. A comparison of the skinfold method with extent of "overweight" and various weight-height relationships in the assessment of obesity. Brit J Nutr 38:271-284.

Wood, R. J. 1981. Insecticide resistance: Genes and mechanisms. IN: J. A. Bishop and L. M. Cook, eds., Genetic Consequences of Man-Made Change. Academic Press, London, pp. 53-96.

Wright, S. 1931. Evolution in Mendelian populations. Genetics 17:97-159.

Wright, S. 1948. On the roles of directed and random change in gene frequency in the genetics of populations. Evol 2:279-294.

Wright, S. 1978. Evolution and the Genetics of Populations: Vol. 4. Variability Within and Among Natural Populations. University of Chicago Press, Chicago.

Wright, S. 1980. Genic and organismic selection. Evol 34:825-843.

Zeng, Z. 1988. Long-term correlated response, interpopulation covariation, and interspecific allometry. Evol 42:363-374.

AFTERWORD

One of America's most successful publicly-owned business corporations, Berkshire Hathaway, uses part of each annual report to advertise its search for additional companies that might wish to be acquired. The explicit corporate strategy is to use profits from existing businesses for reinvestment in companies that might augment Berkshire's already impressive strength into the future.

A comparable strategy is offered here. The gains from a scientific research project are measured not in dollars, but in the acquisition of new knowledge that is useful and interesting-- perhaps even exciting. We seek, therefore, to use the findings presented here to build the strength of our research operation for the future, not only by acquiring financial resources necessary to support additional research, but by attracting new members to our research team.

The work described in the antecedent monograph remains unfinished in many ways. Some data already collected still await analysis, and further studies are suggested by the results already obtained. Some of these future initiatives could even evolve into new subdisciplines. In such a setting, we can promise the challenge of discoveries yet unknown, and can offer for certain only the satisfaction and freedom from ennui that follow from hard work. Prospective student colleagues who find these terms attractive should contact the project director.

Robert B. Eckhardt
Laboratory of Evolutionary Genetics
Department of Anthropology
The Pennsylvania State University
University Park, Pennsylvania 16802