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ABSTRACT

AN ASSESSMENT OF HIGH ALTITUDE GRASSLANDS IN ECUADOR AS A RESOURCE FOR LIVESTOCK PRODUCTION

By

Kim Alyn Wilson

There are vast areas of high altitude grassland in Ecuador, known locally as páramo, that are unused presently but support the growth of forage, principally Stipa Ichu, throughout the year. This land could be used as a resource for livestock production.

The research was conducted in cooperation with the National Institute of Agricultural and Livestock Research at its high altitude experiment station near Quito. Forty-eight Holstein males, weighing 120-438 kg and 6-28 months old, were divided into two equal groups and maintained in pastures at 12,000 and 13,800 feet of altitude for twelve months. During this time a study was made of changes in body weights, blood minerals, red blood cells, forage nutrient composition, forage minerals, forage digestibility and soil constituents. The effect on these measurements of feeding a balanced mineral mixture was an integral part of this study.

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The soil contained high quantities of calcium, magnesium, iron and organic matter. Potassium, copper and zinc concentrations, and pH were normal. There were deficiencies of phosphorus and manganese in the soil.

The principal mineral deficiencies in the forage included calcium, phosphorus, magnesium, potassium and copper. The forage was high in manganese, cobalt and zinc. The sodium concentration was normal.

The results of blood mineral analyses showed that sodium, potassium and iron were above normal sea-level values. Serum magnesium concentrations were normal. The levels of calcium in the serum were below normal values measured at low altitude.

The mean packed-cell volume of the blood increased steadily during the trial. Hemoglobin-bound iron values were slightly below those of sea level indicating that hemoglobin concentration did not increase with altitude. Because blood volume, red blood cell numbers and total hemoglobin increase with altitude, the oxygen-carrying capacity of the blood was sufficient to compensate for the reduced partial pressures of oxygen at high altitude.

Although mineral imbalances were apparent, classical symptoms of specific mineral deficiencies in the animals were not observed. Skeletal degeneration, lethargy, rough hair coats, periodic lameness and staggering occurred prior to mineral supplementation.

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Even though these symptoms often are indicative of mineral deficiencies, they are not fully diagnostic of mineral imbalances in livestock. The severity and occurrence of these symptoms, however, were reduced notably during a period of dietary supplementation using a balanced mineral mixture.

There was a substantial mortality rate. Among the nineteen steers that died, fifteen were under eighteen months of age. Ten animals died from disease and nine deaths were due to falls over a high cliff or into a deep erosional chasm.

Brisket disease, a common disorder in bovines at high altitude, was not a problem in this trial. Mild symptoms of the disease were detected occasionally but no deaths were attributable to the disorder.

Despite the deficiencies of minerals and the high mortality rate, the survivors were able to gain body weight consuming only the native forage, water and trace-mineralized salt. The rate of body weight gain was enhanced appreciably when a mineral mixture, balanced to meet metabolic requirements, was fed to the steers.

It is concluded from this study that the problems of maintaining livestock at high altitude are more a function of nutritional stress and less due to the stress of reduc

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stress of reduced partial pressures of oxygen. The shortage of quality nutrients at high altitude must be alleviated in order to utilize the region efficiently.

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AN ASSESSMENT OF HIGH ALTITUDE GRASSLANDS IN ECUADOR AS A RESOURCE FOR LIVESTOCK PRODUCTION

By

Kim Alyn Wilson

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Dairy Science

1975

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ACKNOWLEDGMENTS

Because of the duration, location and scope of this research, the list is long of those who have contributed to its fruition.

The author expresses sincere gratitude to his major professor, Dr. Robert M. Cook, for continual counsel, encouragement and interest during the course of graduate study. His inspiration contributed immensely to the personal development of the author.

Sincerest appreciation is extended to Dr. C. W. Minkel, Associate Dean of The Graduate School and Professor of Geography, for his counsel and support as a member of the author's guidance committee. His enthusiasm has contributed greatly to the author's career interest in Latin American Studies.

The author is grateful to Dr. Clinton E. Meadows, Professor, Department of Dairy Science and Dr. John M. Hunter, Director of the Latin American Studies Center and Professor of Economics, for their guidance and constructive criticism in the preparation of this dissertation.

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Thanks are extended to Dr. C. A. Lassiter, Chairman of the Department of Dairy Science, for his interest and counsel throughout the period of graduate study, and for financial support through a Graduate Research Assistantship. The author is grateful to Mrs. Kay Butcher for her assistance during graduate study. The invaluable assistance of Dr. Roger R. Neitzel for computer analysis is appreciated.

Appreciation is extended to Dr. Irving R. Wyeth and Dr. Kirkpatrick Lawton for their long-term interest in the research program.

In Ecuador, the personal interest and cooperation of Ing. Fabian Portilla R., former Director General of the National Institute of Agricultural and Livestock Research (INIAP) is deeply appreciated. The immense dedication of Ing. Portilla and the staff of INIAP assured the success of this research.

The interest and support provided by the present Director General of INIAP, Dr. Enrique Ampuero P. is appreciated. The minds and hands of the following people have contributed immensely to the research project: Dr. Toni Rihs, Director of the Swiss Mission at INIAP, Dr. Gustavo Vera, Director of the Santa Catalina Experiment Station, Dr. Jorgé Roman, Ing. Luis Manosalvas, Ing. Orlando Molina, Dr. Bolívar Espinoza,

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Dr. Jorgé González, Sr. Ricardo Rodriguez, Ing. Juan Sánchez, Sr. Juan Iturralde, Sr. Pedro Anacleto, Ing. Wilson Cajiao, Ing. Telmo Oleas, Ing. Vicente León, Ing. Walter Estrella and Sra. Pilar de Vela.

Sincere appreciation is extended to Ing. Carlos Ruales and Ing. Reuben Espinoza for the gracious donation of their land for the experiment.

The assistance of Mrs. Connie Detering in sampling and laboratory analysis was of immense value. Thanks are extended also to Dr. David Nelson for his interest and counsel during the experiment.

The professional staff of the University of Florida Mission to INIAP provided invaluable counsel and assistance. Deepest gratitude is extended to Dr. Kamal Dow, Mission Director, Dr. John Southcombe, Dr. Roland Poultney and Dr. Michael Schwartz.

The author is grateful for the support and interest of the staff of the Latin American Teaching Fellowships Program of the Fletcher School for Law and Diplomacy at Tufts University. The fellowship contributed greatly to the entire experience in Latin America.

And last, but in no way least, the deepest of appreciation goes to my wife, Dale, for her continual support and for her sacrifices throughout my educational program.

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CHAPTER I

INTRODUCTION

> Yet despite all my preparations, when I went up the highest part of the range called Pariacaca, almost immediately I suffered anguish so severe that I had the idea of throwing myself from the cavalcade on to the ground . . . at the same time I retched and vomited so violently that I thought I was dying, because after throwing up food and phlegm, then bile and more bile, some yellow and some green, I finally vomited blood, on account of the violence which my stomach was suffering. If this had lasted I should certainly have perished but it did not continue for more than three to four hours until we had descended a considerable distance and arrived at a more suitable climate (147).

This vivid account, written in 1589 by a Spanish missionary in Peru, describes accurately the extremes of discomfort that can be experienced at high altitude.

Investigators of high altitude metabolism consider that a condition of stress exists for most organisms when they are subjected to either a true or simulated altitude of 5,000 feet or more. The stress is heightened as the altitude increases. The primary stress factor is a deficiency of oxygen, known as *hypoxia*.

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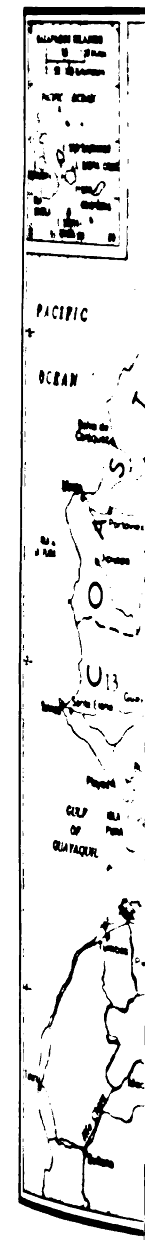
Almost all previous research on high altitude phenomena has focused on the physiological aspects of abnormal performance due to hypoxia. There is, however, little information available on the nutritional aspects. The interdependence of nutrition and physiology in metabolic efficiency in environments below 5,000 feet of altitude has been well established. One purpose of this study was to investigate the role of nutrition in some of the various dysfunctions of high altitude metabolism.

There are vast areas of open range land in the temperate zones of the Andes that are currently under a low level of production. The southern Andean countries of Peru and Chile have high altitude desert areas with small irrigated valleys. In Ecuador much of the land is suitable for crop and livestock production. There are ten major intermontane basins which generally receive adequate rainfall and suffer only moderate dry periods. Most of the cool-temperate zone crops such as cereals, corn, potatoes and onions, and pastures of grasses and legumes, are grown in the basins.

The study was conducted in the Andes Mountains of Ecuador. The country is located on the equator on the west coast of South America. It is divided into three climatic zones (Figure 1): (1) the coastal plain, which lies between the Andes and the Pacific Ocean;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(2) the _sierra_, formed by the Andes and extending north to south in the middle of the country; and (3) the _oriente_, located east of the _sierra_ and forms the western part of the Amazon Basin. The Galápagos Islands, a minor agricultural zone, but a major tourist area, lie approximately 650 miles west of the Ecuadorian coast. The population exceeds six million inhabitants, evenly divided between the coastal and mountain areas. The country is in the beginning stages of industrialization. Yet, it is greatly dependent upon agriculture. The physiographic and climatic diversity provides the country with the potential to produce many kinds of agricultural products.

There are shortages of milk and meat products in Ecuador and the other Andean countries. There are more than 1,000,000 dairy animals in the Ecuadorian _sierra_, including about 300,000 milking cows. The average daily milk production per cow is six pounds, compared with more than thirty pounds in the United States. Most of the milk is marketed in the major metropolitan areas with little reaching the rural Indian population. The average annual per capita consumption of milk is about thirty-five quarts. Part of the milk produced is marketed as cheese and some is fed to calves. Most of the meat production occurs on the coast and some is produced in the higher altitudes of the eastern forest region. The

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region. The average annual per capita consumption of beef is approximately thirty-seven pounds. The meat is of poor quality because the grading standards and pricing incentives to produce high quality meat have not been developed.

Livestock production in the sierra is based primarily on pastures, although there is some reliance on concentrates, especially for swine and poultry production. Meat production is based on the ruminant (e.g. dairy and beef cattle, sheep) and limited use of swine and poultry.

The management practice of the dairy farmer in the Ecuadorian sierra can be discussed in general terms because of its simplicity. The system is based on pasture, but some grain feeding occurs. The primary energy source for milk production is grass pastures consisting of various ryegrasses, some orchard grass, timothy and bluegrasses. On many of the farms using improved management practices, some legumes are included in the pastures, with the clovers, alfalfa and vetches being the principal plants. A considerable amount of fertilizer, usually of high phosphorous content, is used in the sierra.

The low productivity of dairy cattle in Ecuador is due to several factors. Almost all of the dairy cattle in the sierra are crosses of Holstein-Friesian

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and the native criollo cattle. A small percentage of the dairy cattle are purebred Holstein-Friesians. The average age of dairy heifers at first calving is thirty-six months, compared with twenty-four months in the United States. This is due, in part, to poor nutrition which reduces the growth rate and can affect fertility. The animals are small at the age of fifteen months, with an average body weight of 650 pounds, which compares with the goal of 750 pounds at fifteen months in the United States. Delayed breeding is due also to the low fertility of the bulls and the limited amount of semen available for artificial breeding. Poor estrus detection and incorrect timing of breeding or insemination are also major factors. These conditions play a role in the extended calving interval, which is estimated at fifteen to eighteen months as compared with twelve to thirteen months in the United States. Inadequate reproductive efficiency, a low plane of nutrition and a prevalence of mastitis and disease cause a high culling rate. The rapid turnover of milking animals is about equal to the production of herd replacements. As a result, the national milking herd is increasing at a very slow rate, less than 1 percent annually.

A common practice in the management of herd replacements is to nurse the calves on dams for several month

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several months. If this practice were followed by an adequate feeding regime after weaning, the time required to reach an acceptable breeding age or weight would be considerably reduced. However, the replacements are weaned to poor quality pasture and suffer a prolonged weaning check. The practice of grazing the young stock ahead of the dairy herd is employed occasionally, but many herds suffer from lungworm and the young stock follow the cows with a consequent contraction of adult infections. The emphasis of management practices is on milk production, with little attention paid to the benefits of good young stock management.

A major decision to be made in dairy herd management involves the utilization of male animals, normally about 50 percent of the total calf crop. The use of male cattle is one focus of this study and is a major management problem in Ecuador and most other developing countries. In Ecuador the male animals are usually sent to slaughter within three days of birth. A bull calf is saved occasionally for use as a herd sire. On some of the better farms the bulls are castrated and milk-fed for veal. This is an expensive system and, although there is some demand for veal, the pricing incentives are not sufficient to encourage such utilization of the milk. One of the primary reasons given for not using the male animals for meat production is the lack of available nut

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available nutrients. The limited available nutrients for milk production apparently cannot be spared for long-term meat production.

The apparent lack of nutrients is mostly a reflection of poor management practices, since pastures are not utilized efficiently. Simple improvements in management of the available forage can accommodate a significantly larger cattle population. Land use in the sierra is not intensive. For areas in dairy production it is estimated that there is an animal carrying capacity of about one-half to one cow-equivalent per hectare. If proper pasture mixtures and management practices were adopted, the potential carrying capacity could be increased to almost four mature-equivalent head per hectare. Recent data indicate that if the farmers were only to adopt a recommended grazing interval of twenty to thirty days, instead of the present fifty to seventy days, milk production could easily be doubled and at least one-half of the present land in pastures could be put into other crops or utilized by additional cattle (144, 145). This increase in milk production is based on a technological change. Unfortunately, an economic analysis was not included. The efficiency of agricultural production includes economic factors as well as technological factors. Livestock production in the Andes has depended on native herbage for centuries.

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centuries. In recent years improved varieties of forage have been both imported and developed locally.

The study was conducted in cooperation with the National Institute of Agricultural and Livestock Research of Ecuador (Instituto Nacional de Investigaciones Agropecuarias, INIAP). This organization is a semiautonomous body under fiscal control of the Ministry of Agriculture, which contributes a large part of the annual budget. INIAP also receives grants and loans from outside lending agencies, such as the World Bank and the Rockefeller Foundation.

The function of INIAP in Ecuador is similar to that of the Agricultural Experiment Station system of the United States. The major portion of Ecuadorian agricultural research is conducted by INIAP. The Ministry of Agriculture also conducts research, much of which is in the field of animal health. Extension Service activities are likewise conducted by the Ministry. INIAP consists of five major experiment stations, located so as to facilitate investigation of the technical and practical aspects of production which are reflected by the crops and livestock characteristic of the zone. There are four major stations on the coastal plain and one in the *sierra*, plus one smaller unit in the southern *sierra* now undergoing expansion.

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INIAP has developed rapidly since its beginning fifteen years ago, due largely to the talents and perseverance of its director and staff during this period. The organization has been able to develop research programs and, at the same time, send several of its technicians abroad for graduate training. Many of these men have returned and are now conducting research which complements the national five-year plan for development. Although much more training is needed, the present staff is highly capable and creative, and dedicated to significant agricultural improvement. More than half of the technical personnel has the equivalent of bachelor's degrees. The training of the others is evenly divided between graduate degrees from other countries and no university education.

INIAP initially had the objective of improving agricultural production in Ecuador, but much of the specific research is also applicable to other Andean countries, especially in the mountainous areas common to these nations.

A significant change in the economy of Ecuador occurred in mid-1972 when the country began exporting crude oil. A pipeline from the eastern forest region was constructed over the Andes to Esmeraldas, the major northern seaport. Between 200,000 and 250,000 barrels of crude oil are now exported daily. The government has begun co

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has begun construction of a refinery to eliminate the nation's dependence on imported fuels. The rapid rise in world oil prices during 1973 provided the country with extra foreign exchange earnings.

Since the middle of 1973 the amount of credit available for agricultural inputs has increased considerably. The capital has come from banks, outside lending agencies, the export of petroleum and the elimination of import duties on farm machinery and chemicals. All banks are required to make loans to agriculture and small business amounting to at least 25 percent of their total loans. Although substantial credit is available, world supplies of fertilizer, farm machinery, grains and seeds are critical items in short supply. Major increases in agricultural productivity will be difficult to achieve until world supplies of these inputs become available. Previously, insufficient capital prevented large purchases of agricultural supplies when they were readily available and inexpensive.

Corn and cereal grains are in short supply in Ecuador. Much of the grain has been exported because of high world prices, making it difficult to maintain stocks for domestic use. The government has developed marketing and pricing controls in an effort to increase grain reserves. These crops have longer growth cycles in the _sierra_ than those in the major grain-producing

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Forages are the principal source of nutrients for meat and milk production in Ecuador, due to the shortage of grain. The pastures in the intermontane basins of the *sierra* are used mostly for milk production and for the growth of females as herd replacements.

Approximately 80,000 dairy bull calves are born in the highlands of Ecuador each year. All but a few of the bulls are slaughtered within a few days of birth because they would compete for the limited nutrients available for milk production. These animals are a potential source of meat which is lost because of an apparent lack of alternatives.

Ruminants (e.g. dairy and beef cattle, sheep, goats, llamas and alpacas) are efficient converters of poor quality, highly fibrous forage into high quality products such as meat and milk for human consumption. Most of the forage plants are unsuitable for consumption by humans or for economical production of monogastric livestock.

There are approximately 2,400,000 acres of land above an altitude of 11,500 feet and extending to the rock faces of the mountain peaks above 14,000 feet.

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Only a small part of this land is used, mainly by rural Indians for periodic grazing of sheep, goats and llamas. The area is called the páramo. It is geologically and ecologically similar to the Altiplano in Bolivia, but is steep, undulating and receives more rainfall. The area resembles the bunch-grass prairies of the United States.

The vegetation in the páramo is more than 90 percent grasses. The dominant species is *Stipa Ichu*. It is high in fiber, low in protein and grows slowly. Between 11,500 and 12,000 feet of altitude some clover can be found. Lupines grow at all altitudes in the páramo.

The four factors above (the availability of animals, land and forage, combined with the metabolic characteristics of the ruminant) were basic to the justification of this study. The need to increase meat production for domestic consumption and the desire to investigate the potential of the páramo in meeting this need were expressed by government officials. Thus, the availability of resources, a recognized need and the potential for major agricultural impact form the basis of the investigation. An additional aspect was the author's desire to study the agriculture of a developing country, with a broader goal of gaining perspective on agriculture's role in the process of national development.

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Some of the economic, political and technological features of the environment in which this study was conducted have been discussed. Several factors related to the need for investigating this particular subject have been identified. The latter include:

1. The availability of essential resources in Ecuador, which if managed properly could provide the production of additional meat with a minimum shift of agricultural inputs away from existing production;

2. The suitability of the ruminant for maximum utilization of natural resources;

3. A need to increase meat production for domestic consumption; and

4. An availability of adequate technical support.

The metabolic responses of man and animals to the stress of high altitude and the effect of this stress on productivity have yet to be considered.

CHAPTER II

REVIEW OF LITERATURE

> There is no doubt whatever that the cause of that strange disorder and alteration is the wind or atmosphere that prevails there, because the only treatment found . . . consists in covering the ears, nose and mouth as well as possible, and in clothing oneself well, especially over the abdomen. The air is so fine and penetrating that it enters the intestines. . . . I am convinced that the element of air . . . is so subtle and delicate that it is unsuitable for human respiration, which requires thicker and more tempered air. . . . It is extremely fine and delicate and its cold is not so much sensible as penetrative (147).

During a crossing of the Peruvian Andes in 1589, Acosta not only described the event but he also ventured a theory about the factors that caused his extreme discomfort. His perception that some characteristic of the "air" was a factor has been shown to be correct but, this characteristic is now known to be the reduced partial pressure of air, especially of oxygen. He also perceived the phenomenon as a feature unique to the geographical location rather than one related to the high altitude of the area.

Almost 300 years after Acosta wrote his account, controlled studies of high altitude phenomena and their causes had b

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causes had begun and were first summarized by Bert in 1878 (19). His review of the limited information existing at the time concluded that "oxygen deficiency is the main feature in all biological effects of a decrease in barometric pressure."

A principal factor affecting the data of this study is reduced barometric pressure or, more specifically, reduced partial pressure of oxygen (hypoxia). Therefore a review of the literature should emphasize hypoxia and its relation to other relevant factors. When considering any aspect of the study (e.g. the productivity of livestock, soil and plants, or economic and social ramifications), it is noteworthy that animals, as well as man, are continually exposed to the stress of hypoxia in the sierra of Ecuador. Hypoxia may pose constraints that greatly affect livestock production or the learning process and social behavior of man. It may also alter some physical norms and concepts which have been established by studies conducted in the most populous stratum of the world, the area below 5,000 feet elevation.

The exposure of man and animals to hypoxia affects their homeostasis. Homeostasis is a tendency of the body to maintain internal physiological and metabolic stability in response to conditions that disturb the normal functions of the body. The degree to which the

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to which the organism adjusts to the stress of hypoxia depends on the extent and duration of the stress, the species and nutritional status (269, 275).

The literature reviewed covers three main areas:

1. The nutritional and physiological aspects of hypoxia;

2. The implications of metabolic changes related to the practical aspects of livestock production; and

3. Some pertinent, although limited, information derived from studies conducted at high altitude in South America.

Changes of Tissue Constituents During Exposure to Hypoxia

Hypoxia is a condition of diminished oxygen supply (269). The term usually refers to the atmospheric or ambient conditions of low barometric partial pressure with respect to oxygen. Atmospheric conditions above 5,000 feet in elevation are considered hypoxic. Hypoxia also is used to define the existing condition at tissue and sub-cellular levels. Expressions synonymous to hypoxia include low (or reduced) oxygen tension, oxygen want, oxygen lack, oxygen deprivation and oxygen deficiency. The term "anoxia" is used interchangeably with "hypoxia" by some authors, but it is unsuitable

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because it literally means the absolute lack of oxygen. That, of course, is a state not encountered at any terrestrial altitudes under normal conditions (269).

The principal stress of man and animals at high altitudes is decreased atmospheric oxygen pressure. The hypoxia of high altitude can be simulated in decompression chambers at any terrestrial altitude. However, these are most often used at low altitude to study the effects of hypoxia when it is inconvenient to conduct the experiments at high altitude locations. Most studies using simulated altitudes produce hypoxia by reducing the barometric pressure in the chamber. A few experiments include a reduction in the oxygen concentration while barometric pressure remains normal.

The definition of the physiologists with respect to hypoxia is a deficiency of oxygen in the inspiratory air of the organism under study. Due to a variety of factors, hypoxia can cause an oxygen deficiency in tissues other than pulmonary alveoli. For example, anoxic hypoxia (hypoxemia) is a condition in which there is an oxygen deficiency in the arterial blood and the hemoglobin is not saturated with oxygen. Anemic hypoxia describes blood as having normal levels of oxygen with abnormally high amounts of circulating hemoglobin. In stagnant hypoxia there are normal amounts of oxygen and hemoglobin in the blood, but the oxygen is not given up to the tiss

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In addition to the above forms of hypoxia each one can be further delineated as either acute or chronic (269). The acute hypoxias occur rapidly and most often accidentally, such as losing pressure in aircraft at high altitude or inhaling oxygen-free, physiologically inert gases such as nitrogen or methane. Although all systems of the body can be affected by acute hypoxia, the most sensitive are the central nervous, pulmonary and circulatory systems.

The chronic form of hypoxia is experienced by organisms living for moderate to long periods at high altitude, or by repeated exposure to subnormal supplies of oxygen. Depending upon the ability of the organism to become acclimatized to increased altitude, and the duration of the exposure, degenerative changes in certain organs may be produced. Barcroft has suggested that chronic hypoxia resembles mental and physical fatigue (14).

Hypoxia has its direct effect through reduced partial pressure of oxygen, and not through lowered barometric pressure *per se* (10, 269). The barometric pressure at sea level is 760 mm of mercury (Hg), and the percentage of oxygen is 20.96. Therefore the partial pres

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partial pressure of oxygen at sea level is 159 mm Hg. In comparison, at an elevation of 14,000 feet the percentage of oxygen remains at 20.96, but the partial pressure of oxygen is 94 mm Hg, which is only 60 percent that of sea level.

The variables affecting the response of humans and animals to hypoxia were summarized individually by Van Liere and Stickney as: (1) the suddenness of the production of oxygen want; (2) the severity of oxygen want; (3) the duration of oxygen want; and (4) the physical condition of the body (269).

The environmental variables at high altitude which may influence physiologic processes also were listed by Van Liere and Stickney: (1) lowered atmospheric pressure; (2) reduced partial pressure of oxygen; (3) temperature; (4) humidity; (5) increased intensity of sunshine; and (6) electrical conditions (269). The most important of these factors is the lowered partial pressure of oxygen, whereas the others may play subordinate roles.

It is regretable that Van Liere and Stickney, as authors of an excellent textbook on hypoxia, ignored the possible role of nutrition or nutrient status in the above list of variables affecting physiologic processes. It is a contention of this dissertation that diet or nutrient quantity and quality can significantly modify the

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Carbohydrates and Metabolic Intermediates

Hypoxia alters carbohydrate metabolism in a variety of ways. The primary effects of hypoxia on carbohydrate metabolism are decreased glucose oxidation to carbon dioxide and a reduced utilization of glucose via the pentose shunt (25). These changes are directly associated with the metabolism of hexoses, since the metabolism of intermediates in the glycolytic pathway are not affected by hypoxia.

Glucose tolerance is increased in conditions of severe hypoxia in animals (88, 152, 239, 274) and to a lesser extent in man (164, 225). Keyes and Kelley stated that their studies on dogs exposed to simulated altitudes of 18,000 and 24,000 feet indicate that glucose is converted to glycogen, which signifies an increase in glucose tolerance (152).

Blood sugar levels in the dog, sheep and goat rise rapidly after exposure to high altitudes (269). A significant increase occurs in dogs even after exposures of only fifteen minutes to simulated altitudes of 24,000 feet and above (239). The most dramatic elevation of blood sugar is observed in the goat, followed by the response of the sheep (40, 240, 241). These changes rep

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changes reported by Stickney and associates were more than twice those of the dog, suggesting that the ruminant may be more sensitive to hypoxia than monogastric animals. After three weeks' exposure to moderate altitudes blood glucose is normal or slightly reduced in mice (25).

There are significant changes during hypoxia in glucose utilization by the liver, heart and muscle of the rat (26). The alterations are mainly a decrease in glucose oxidation to CO_2 and reduced utilization of glucose via the pentose phosphate pathway (25). In the rat, over one-third of the glucose was unaccounted for, suggesting that liver glycogen and blood sugar values are not adequate indices of carbohydrate metabolism (26). Glucose carbon can be incorporated into noncarbohydrate compounds such as triglycerides, phospholipids, amino acids and nucleic acids. These may be of importance in describing overall glucose metabolism at altitude.

Glucose may protect or regulate surges of free fatty acid mobilization brought on by the stress of hypoxia. This protection occurs because acetyl CoA may be bound as forms of long-chain acyl CoA compounds. This would interfere with the oxidative decarboxylation of pyruvate to acetyl CoA.

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Glycogenesis is increased in the liver, heart and muscle of animals chronically exposed to high altitude (26, 252). The deposition of glycogen in the liver is variable, depending on the species and the hypoxic duress (269). The storage of tissue glycogen reduces the amount of glucose available for utilization by other major pathways.

It is well known that lactic acid develops in the blood during exercise. Studies in the 1930's demonstrated that lactic acid levels in the blood are not elevated due to the stress of high altitude. In fact, after severe exercise at 12,000 feet, blood lactate was lower than that found after comparable exercise at sea level. It remained lower after the same exercise at 15,000 feet, and above 20,000 feet the lactate was only slightly above sea level values (28, 72, 77). It is thought that this behavior of lactic acid may be a protective mechanism during work or exercise at altitude (70). Hurtado stated that lactate and pyruvate production at altitude is unchanged from sea level values when the body is at rest (140). However, the production of both acids declines with strenuous activity at altitude while there is little change at sea level.

Under normal oxygen conditions the changes in blood lactate correspond closely with changes in blood pyruvate (1

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pyruvate (135, 136). However, during anoxic hypoxia the level of lactate increases relative to pyruvate (135, 136). Since there is little change in lactate *per se*, as noted above, it is probable that a decline in blood pyruvate levels occurs. This phenomenon is not clearly understood (269).

A main feature of carbohydrate metabolism at high altitude is an increase in glycogenesis, which causes a reduction of glycolysis. This, combined with a decline in acetyl CoA because of binding by fatty acid mobilization, may account for the decline of the conversion of pyruvate to lactate during exercise at high altitude.

The absorption of glucose from the small intestine of dogs is slightly increased, but not significantly, when they are subjected to simulated altitudes of 27,000 feet (202). Although it has been shown in numerous studies that glucose absorption is a process of active transport under normal conditions, only complete hypoxia, or anoxia, will affect the ability of the intestine to absorb glucose under in vitro conditions (269).

Lipids

The few reported studies suggest that responses are variable with respect to the effect of hypoxia on blood lipids. Plasma phospholipids have been shown to decrease in

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decrease in rabbits (244). In one study blood cholesterol increased (226). There are no reported cases of hypercholesterolemia in acclimatized Andean residents (139). MacLachlan conducted an extensive study which demonstrated that cats and dogs exhibit an increase in blood lipids with altitude, whereas the rabbit shows a decline (178).

Hypoxia results in hypertriglyceridemia in rats. Possible mechanisms have been suggested by Chiodi and Bass (51). In hypoxia, the abnormally high release of triglycerides by the liver is faster than the adipose tissue can absorb them. Or, perhaps there is a decrease in the ability of adipose tissue to store those triglycerides entering the plasma at a normal rate. A third suggestion is that there may be an impairment of triglyceride synthesis by the adipose tissue. Chiodi and Bass conclude that low lipid utilization is a complex process with a low rate of resynthesis in adipose tissue, caused by a low glycerophosphate supply. Glycerophosphate is stimulated by carbohydrate intake and is needed by adipose cells for glyceride synthesis. This could explain the excess of plasma lipids and their consequent abnormal deposit in the liver.

A study of serum lipid components in humans consisted of an adjustment period at sea level for fourteen days, followed by a period of nine days at

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14,100 feet (278). Compared with sea level the high altitude period resulted in a decrease of caloric intake during the nine days; an increase in serum-free fatty acids the first day, which remained for the nine days; a steady weight loss; a significant and continued increase in triglycerides after day six, and a significant negative correlation between serum-free fatty acids and caloric intake. As a result of mobilization of fatty acids from the triglyceride pool, in the adipose tissue the percentage of linoleic acid decreased while palmitic and oleic acids increased in both the free fatty acid fraction and the triclyceride fraction. The authors concluded that there is a direct effect of caloric restriction on serum free fatty acids. These changes of serum lipids in humans abruptly exposed to 14,100 feet altitude probably reflect neuroendocrine alterations in the mobilization of stored lipids with concomitant decreases in body fat.

According to Surks et al. (245) and Whitten and Janoski (278) high altitude exposure is accompanied by a decrease in body weight which is primarily due to fat loss. However, studies with rats show that oxygen consumption increases at altitudes of 14,100 or 20,000 feet when expressed per unit of lean body mass or cell mass (49). The change occurs primarily in the lean mass and is

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Rats exposed to simulated altitudes ranging from 8,000 to 18,000 feet showed no differences in fat absorption over sea level exposure (181). However, from 24,000 to 28,000 feet there was a significant reduction in fat absorption. Also, between 5,280 and 14,100 feet there appears to be either a decrease in fat absorption, or a decline in apparent fat digestion, or both (49). This latter study was not designed to distinguish between the two effects.

Gloster et al., using pair-fed rats exposed to high altitude, reported there was a decrease in total right ventricular lipid and triglyceride (98). However, there were no differences in pulmonary lipids or cardiac phospholipids. There was a significant decline in myocardial cholesterol and cholesterol ester, regardless of treatment in older rats, which was seen as a reflection of diet.

The data of Rasmussen clearly show that in rabbits lipids are accumulated in the myocardium and renal tubular cells within forty-eight hours after the onset of starvation (214). MacLachlan demonstrated that there was no effect on blood lipids when cats and dogs were starved in high altitude conditions and blood lipids in rabbits declined (178).

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High altitude conditions have been associated with a pronounced increase in the following cardiac lipids: total myocardial lipids (rabbit, dog, guinea pig); phosphatidic acid (rabbit, dog); phosphatidyl ethanolamine (rabbit, dog); sphingomyelin (rabbit, dog, guinea pig); lysolecithin (rabbit); phosphatidyl choline (rabbit, dog); phosphatidyl inositol (rabbit, guinea pig); phosphatidyl serine (rabbit, guinea pig) and cholesterol (rabbit, dog, guinea pig) (99). Total neutral lipids were higher in the rabbit, lower in the dog, and not significantly different from sea level values in the guinea pig. The percentage of saturated fatty acids in phospholipids was significantly lower at altitude for all three species, as was the triglyceride content.

Grice and coworkers recently demonstrated the effect of excess cobalt on myocardial function and lipid metabolism (115). It is well known that under normal conditions rat myocardium oxidizes long chain fatty acids for its energy requirements in preference to pyruvate or glucose, and in the absence of these long chain fatty acids pyruvate is greatly preferred. However, excess cobalt administrated intraperitoneally to rats significantly decreased the ability of the myocardium to oxidize octanoate and pyruvate (73, 263). This resulted in degenerative heart lesions associated with incre

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with increased myocardial lipid and ground substance and decreased myofibrils. Based on this information it is difficult to understand the protective effect provided to an animal under hypoxia when treated with cobalt chloride. It appears that the condition of hypoxia combined with cobalt therapy would increase cardiac and systemic lipids beyond a level beneficial to the animal. Diet quantity and quality should play a major role in these phenomena. But, little emphasis has been placed to date on the role of nutrition and its interaction with lipid metabolism during hypoxia.

The main feature of lipid metabolism during exposure to hypoxia is an increase in blood lipids caused by neuroendocrine changes. The mobilization of fatty acids causes a loss in body weight and an increase in the deposit of fat in the liver. There is a change in the fatty acid composition of lipid components and an increase in phospholipids. The normal contribution of energy by carbohydrates is reduced and compensated by increased lipid metabolism.

Proteins and Nonprotein Nitrogen

There is a dramatic increase in serum protein levels when the net change of altitude is 8,000 feet or more (269). High altitude exposure is often associated with a negative nitrogen balance in man and rats, due

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mainly to a decrease in serum amino acids and an increase in the turnover of serum albumin (154). When rats were exposed to an altitude of 14,110 feet for thirty days there was no effect on tissue storage of amino acids. Klain and Hannon determined that an acute exposure to hypoxia results in a transitory increase in protein catabolism (154). Early studies indicated that the levels of nonprotein nitrogen in the blood do not change with terrestrial altitude (269).

The absorption of glycine is significantly decreased by hypoxia equivalent to altitudes greater than 23,000 feet (202). Only in complete hypoxia or in cyanide poisoning (histotoxic hypoxia) is transport limited for the L-forms of methionine (280), alanine (91) and histidine and phenylalanine (3).

It has been demonstrated that anoxic hypoxia causes a decrease in the excretion of ammonia (65, 118). It is thought that the decrease is a response to alkalosis. However, Brunquist observed an increase of total nitrogen excretion (urea, ammonia, creatine) in severe hypoxia, which was similar to the increase in urinary nonprotein nitrogen observed in fasting rats in hypoxia (32). This phenomenon may be a reflection of an increase in gluconeogenesis from protein during hypoxia (269). In natives of sea level compared with natives of high altitude,

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altitude, there were no significant differences in muscle tissue (216).

The most significant changes in protein metabolism are observed as alterations of enzymes.

Enzyme Activity

The activity of several enzymes increases in hypoxia. Among these are transhydrogenase, NADPH-cytochrome C reductase and the mitochondrial NADH-oxidase system as reported by Hurtado (140, 141). The results of a study of rats by Klain and Hannon indicate that rats exposed to an altitude of 14,110 feet had significantly higher hepatic arginase and hepatic arginine synthetase activities after two days, but not after thirty days (154).

Hurtado summarized the limited information on the effects of hypoxia on enzyme activity as an apparent increase in oxygen utilization (140). This appears to be operative along the pathways linked preferentially with the production of high-energy phosphate bonds.

Reynafarje studied muscle myoglobin and enzymes in natives of sea level and at an altitude of 14,400 feet (216). Myoglobin was significantly greater at high altitude than at sea level. Muscle NADH-oxidase (whole homogenate), NADPH-cytochrome C reductase and transhydrogenase (24,000 xg fractions only for the latter two enzymes) were all significantly higher in activity a

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activity at altitude than at sea level. There were no significant changes in NADH-cytochrome C reductase, isocitric dehydrogenase or lactic dehydrogenase activities. The author concluded that the respiratory capacity of muscle is apparently higher in the native of altitude compared with that of the sea-level native.

Aspirin (acetylsalicylic acid) feeding to rats exposed to hypobaria has been shown significantly to increase the glucose-6-phosphatase activity in the liver (272). Aspirin also increased liver activities of glutamic oxalacetic- and glutamic pyruvate-transaminases and plasma levels of glutamic acid, but none of these effects were significantly affected by high altitude exposure. Altitude exposure did shift the diurnal variation of blood glucose (glucose was higher, earlier, after feeding), lowered the liver phosphorylase activity, and was associated with lower peak liver glycogen levels. According to the authors, the most important practical aspect of the study with regard to the animal was the lowered hematocrit, which significantly reduced blood viscosity.

Humans treated with metelone acetate and vitamins showed an increase in the activities of glutamic pyruvic transaminase, lactic dehydrogenase and aldolase when blood-sampled at altitudes up to 20,000 feet (5). There was no change in creatine phosphokinase activity due to alt

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Minerals

The effect of hypoxia on mineral metabolism has not been thoroughly studied. Most existing knowledge is derived from research conducted at low altitude. The macro-elements and micro-elements are necessary for a wide variety of biochemical reactions. Few data exist on the requirements for minerals at high altitude.

Little is known about the effects of hypoxia on blood sodium and chloride levels. Available data suggest that there is no significant change (269), although it has been indicated that blood chlorine increases at altitude, while sodium levels are minimally affected (140). Mild degrees of hypoxia reduce the absorption of isotonic sodium chloride solutions in the dog (267). The absorption of sodium chloride in hypoxia is not affected by the presence of sulfate radical, the absorption of which, itself, is not affected by even severe degrees of hypoxia (270).

Under controlled laboratory conditions, potassium levels in the blood appear to decrease rapidly after exposure to anoxic hypoxia (84). This is in contrast with asphyxia, in which blood potassium increases significantly due to its mobilization primarily by the liver

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the liver in response to epinephrine which is rapidly secreted by the adrenal glands (43, 69, 282). However, Hurtado suggested that the change in potassium is minimal at altitude (140).

After a two-week sea level control period, humans were subjected to nine days at 14,100 feet and were maintained on a constant sodium and potassium intake (146). A decrease of urinary potassium excretion and an increase in serum potassium were observed. No changes were noted for sodium concentration in urine or serum. Since Luft et al. showed that maximum oxygen uptake is directly related to muscle potassium content (173), the retention of potassium during hypoxia may be a protective mechanism.

The levels of calcium in the blood of humans appear to be similar regardless of altitude (140). According to Hurtado in 1964, no research at high altitude on the levels of magnesium and sulfate radical have been reported (140). An increase of phosphorus in the blood occurs during hypoxia. The change primarily is in the level of 2,3-diphosphoglycerate, the major red blood cell phosphate. This chemical regulates the affinity of hemoglobin for oxygen and its availability to tissues (165, 204). The level of 2,3-diphosphoglycerate in humans returned to normal after one week of exposure to an altitude of 14,300 feet.

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Under normal barometric conditions iron deficiency increases the accumulation of magnesium in the kidney, liver and testes of rats (44). The increases range from 2.0 to 2.5 times the control levels when the rats consume a normal intake of iron. It is expected that high altitude would aggravate the effect of iron on magnesium metabolism.

In an Ecuadorian study, fifteen patients with iron deficiency anemia were transported from an altitude of 4,000 feet to Quito, at an altitude of 9,300 feet (168). After exposure to the new altitude, all of the subjects showed pronounced increases in hemoglobin, hematocrit, red cell number and volume, blood volume and total plasma iron. Decreases were noted in plasma volume and iron disappearance time. No change in red blood cell turnover time was observed. These changes are also observed upon ascent to even greater altitudes. An iron-deficiency anemia existing at low altitude can be aggravated when the anemic patient is exposed to hypoxia. Central American natives have major deficiencies of folic acid and vitamin B_{12} (86). These hemopoeitic factors were probably involved in the etiology of the anemias found in Central America and were due to consumption of diets in which 75 percent of the calories were from carbohydrates and very few were from animal products.

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Vitamins

Chicks and hens raised on a diet enriched with 60 mg of vitamin E per pound of feed demonstrated a significant increase in resistance to disease (248). When they were exposed to a simulated altitude of 15,700 feet the immune response was significantly greater, suggesting a synergistic effect of hypoxia and vitamin E. The authors indicated that perhaps the vitamin E was acting as an antioxidant and, combined with hypoxia, created greater reducing conditions in the electron transport chain for cellular development. Resistance to disease in hypoxic, normoxic and hyperoxic conditions is highly variable, with or without vitamin therapy. Schmidt suggests that more work should be done and, for the moment, only one generalization can be made: modified environments may affect host susceptibility to infectious disease (227).

Ascorbic acid levels in the blood are lower in hypoxia in guinea pigs and hamsters, and scurvy develops more readily (29, 31, 116). The ascorbate requirement for man is not increased at altitude (269).

The requirement of man for thiamine is not changed during prolonged exposure to hypoxia (109, 269).

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Greig and Govier stated that extensive dephosphorylation in tissues occurs in hypoxia (114) and may include the coenzyme thiamine pyrophosphate (109). The coenzyme is essential for the oxidative decarboxylation of pyruvate to acetyl CoA and CO_2. Its dephosphorylation would increase thiamine and pyruvate levels in the blood. This is not consistent with the results of studies on carbohydrate metabolism, which showed that a decline in blood pyruvate occurs in hypoxia.

Acid-base Balance

Hypoxia was originally thought to be a problem of acidosis, because of the net production of various blood acids and a decline in alkaline reserves. It is currently considered that alkalosis is the prevailing condition in hypoxia, despite an apparent decline in alkaline reserves (269).

The mechanism of the production of alkalosis at altitude has been summarized by Van Liere and Stickney as follows: hypoxia causes hyperventilation, which decreases alveolar carbon dioxide tension, which in turn produces a lowering of the arterial carbon dioxide tension (269). In an attempt to maintain an acid-base balance in the body, the kidneys secrete more base, especially more plasma bicarbonate. This continues until the reduction in plasma bicarbonate is proportional to the re

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to the reduction in carbon dioxide tension. The net effect is a slight increase in blood pH. Most recent data indicate that alkalosis occurs at altitudes up to about 12,000 feet. Above this altitude there is either little change or a return to normal. Unless severe conditions exist, alkalosis is produced.

Von Muralt reported that a well-established fact of high altitude physiology is the development of acapnia (loss of CO_2) in the blood, which leads to respiratory alkalosis (274). Acapnia occurs within one day after arrival at high altitude and rapidly disappears as acclimatization proceeds. This mechanism of alkalosis is in agreement with the summary by Van Liere and Stickney (269). However, the mechanism does not fully explain the respiratory alkalosis resulting from high altitude exposure, because after returning to sea level an increased sensitivity of the receptors for CO_2 remains for weeks and, in some cases, even months (274).

Physiological Changes During Hypoxia

The stress of hypoxia affects several homeostatic mechanisms. The organs most sensitive to hypoxia are the lungs, heart and kidney. Much of the sensitivity is directly related to the hematological changes in the circulatory system. The endocrine and central nervous systems also are disturbed by hypoxia.

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One of the most dramatic and rapid changes in the blood in hypoxia is polycythemia, i.e. an increase in the number of circulating red blood cells, both for erythrocytes and reticulocytes (10, 37, 75, 82, 141, 269). This polycythemia has been shown to be due primarily to oxygen insufficiency, rather than to diminished barametric pressure *per se* (62, 140). Dallwig et al. demonstrated as early as 1915 that reduced total oxygen in inspired air, whether due to lowered barometric pressure or to a reduction of the concentration of oxygen while maintaining sea-level barometric pressure, was associated with a significant polycythemia (62). Their study was performed using several species, and the results have been confirmed by a myriad of authors. Under conditions of chronic hypoxia it is known that the polycythemia is not as dramatic and is closely related to other changes in blood components.

Carbon monoxide inspired in sufficient quantity to saturate the hemoglobin up to 33 percent can produce a marked polycythemia (198). However, carbon dioxide has a lowered partial pressure at high altitude which minimizes its erythropoietic action.

Some suggested causes of hypoxic polycythemia may be summarized as follows: (1) an unequal distribution of red blood cells throughout the body; (2) a lengtheni

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lengthening of the life span of erythrocytes; (3) increased irradiation by the more powerful sunlight at high altitudes; (4) the presence of an auxiliary or latent store of red blood cells; (5) a hemoconcentration at high altitudes; and (6) an acceleration of hematopoietic activity of red bone marrow (269). The first three theories have been shown to have little or no role in hypoxic polycythemia. It is generally believed that polycythemia is due largely to hemoconcentration. In some animals there may be a mobilization of cells from blood stores in the body (8, 110, 142). Although many studies of erythrocyte mobilization have provided results which are inconclusive, some data show that the spleen contracts and releases red cells into the circulation. Collins and Farrell state that the horse and racing greyhound are unique in that they have a significant splenic reserve of erythrocytes which is released, on demand, into the general circulation within a short period (54).

The sixth theory mentioned above by Van Liere and Stickney (269) is valid because it is known that there exists a circulating erythropoietic stimulating factor in animals which have been exposed to low oxygen tension. Also, a humoral factor, called hemopoietine, is involved in the polycythemic response to hypoxia (105, 110).

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The sequence of events in the erythropoietic response of rats has been described by Miller et al. (192). Six hours after subcutaneous injection of rats with 10-25 micromoles of cobalt chloride per 100 grams of body weight, a dose-related respiratory alkalosis occurred, associated with an increase in the affinity of hemoglobin for oxygen, followed by an increase in the production of erythropoietin. In nephrectomized rats, opposite effects occurred after cobalt chloride administration. The kidney appears to be the primary site of erythropoietin production. It is stimulated by a decrease in tissue oxygenation, as a result of the alkalosis which increases the affinity of hemoglobin for oxygen. This decreases the amount of oxygen available to the tissues, resulting in histotoxic hypoxia (80, 192).

The greatest polycythemic change appears during a change in elevation from sea level to 6,000 feet. The rate of change is less above 6,000 feet, although the number of cells continues to increase. This diminution in the rate of polycythemia prevents the blood from becoming excessively viscous, which would place too much strain on the heart while trying to maintain blood circulation. In studies on horses transported to 7,000 feet altitude it was shown that the erythropoietic response was incomplete even after an expos

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an exposure of seven weeks (54). Compared with cattle, which do not show as dramatic an erythropoietic response, horses greatly increase their hematocrit, mean corpuscular volume and mean corpuscular hemoglobin concentration. The increase in cell number and hemoglobin is most dramatic during the first three days at high altitude.

Although the polycythemia reverses within a few hours after return to sea level or low altitude, the time required to obtain a normal blood picture is highly variable. The adaptation period can be as long as six months, depending on individual differences and the time and extent of exposure. Hurtado et al. reported that the blood of persons native to high altitude exhibits the same morphological characteristics after some weeks at low altitude as those found in persons native to low altitude (198).

The size of red blood cells can increase during long periods at high altitudes (74, 139, 142, 171). This is associated with an increase in hemoglobin content of the red blood cells (142). Although macrocytosis occurs in most cases, at times anisocytosis occurs, which is an inequality in the sizes of the cells (171).

Changes in blood volume are highly variable during acute hypoxia and no consistent change has been

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determined. However, during chronic hypoxia there is an increase in blood volume in both man and animals, largely as a result of the expansion of the red cell mass (10, 142, 217). The first evidence of an increase in blood cell volume was reported as early as 1891 in observations at sea level and in the Andes of Peru and Bolivia (273). Viault determined that the red cell concentration at sea level was 5 x 10^6 cells/mm^3, and at 14,890 feet it had risen to 7.5-8.0 x 10^6 cells/mm^3 (273). This was also the first evidence that blood changes occur in a very short time after exposure, rather than during generations of acclimatization as was thought until that time.

The effect of hypoxia on blood volume has been studied in goats (20). Three female goats at six months of age were exposed for eleven weeks to pasturing from 6,100 to 8,230 feet elevation. Their body weight increased continually, except for a depression after being transferred to the high area from an altitude of 1,340 feet. Total blood volume increased significantly as did the body content of the blood, from 6.86 percent of the body weight at the control altitude (1,340 feet) to 7.73 percent at high altitude, and returned to normal (7.03 percent) after an eight-week recovery period at the control level. The reserve blood volume apparently was mobilized during the initial five weeks at altitude, and litt

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and little storage was accomplished. Metabolic adjustments to hypoxia in the remaining weeks permitted an increase in the storage of blood reserves, up to 12.2 percent of the total blood volume. Most of the blood reserves are maintained in the spleen and are released by adrenaline-like compounds.

Grawitz, in 1895, was the first to report that altitude exposure was associated with a reduction in plasma volume (111). The plasma volume generally decreases during acute anoxic hypoxia, but the response is often inconsistent under conditions of chronic hypoxia (82, 269).

It has been clearly shown that body water loss occurs during anoxic hypoxia, which is the primary mechanism in hemoconcentration (8, 142). Stickney found that body weight loss in rats was proportional to the altitude, up to 28,000 feet, under simulated conditions (238). The thresholds for body weight loss in rats via feces lie between 4,000 and 8,000 feet; below 4,000 feet for urinary loss. Lawless and Van Liere determined the water content of the cerebrum, kidney, liver, muscles, skin and adrenal gland in rats subjected to simulated altitudes from 8,000 to 28,000 feet (161). Above 8,000 feet all animals lost weight, but the organ weights changed little except for some water loss from muscle and skin at 18,000 feet. It was conc

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was concluded that the body weight loss was related primarily to hemoconcentration. The interpretation of the results was "that the body, in order to maintain its homeostatic state, allowed the blood, and perhaps the extracellular spaces rather than the tissue cells, to lose water" (161). In rats exposed continuously to an altitude of 15,000 feet, body water loss was greatest during the first week. During this time 20 percent of the body water was lost, accounting for 94 percent of the total body weight loss (209).

During acute hypoxia, body water declines but recovers to normal levels after acclimatization (207). In a 32-day trial with sheep conducted at a simulated altitude of approximately 18,000 feet, water balance was restored by the end of the test period. This was accompanied by a marked increase in extracellular water, little change in plasma volume, a definite increase in basal metabolic rate and a decrease in the respiratory quotient. The sheep adapted well to high altitude in 4 1/2 weeks and stabilized in the environment. In a study with humans, an acute exposure to high altitude conditions resulted in a shift of three liters of body water from the extracellular space to the intracellular space with a concomitant decrease in plasma volume (121). This relative change was maintained during the fourteen days of the study. In comparison

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with several other studies, it would appear that the duration of this trial was not long enough to observe a return to normal of the variables studied.

It has been demonstrated conclusively that there is an increase in the total amount of hemoglobin per unit of body weight during hypoxia. As early as 1913 it was established that in humans of both sexes hemoglobin rises about 10 percent for every 100 mm Hg. decrease in barometric pressure (85). Both the chronic and discontinuous forms of hypoxia increase hemoglobin levels in many species of animals. Total circulating hemoglobin increases more than does the concentration (1, 10, 35, 53, 92, 187, 235). This phenomenon is not clearly understood. The number of red blood cells increases in equal proportion with the hemoglobin (1, 10, 35, 53, 235). As would be expected in hemoconcentration, both the viscosity and specific gravity of the blood increases at high altitude (1, 10, 35, 53, 235). The normal value in man is 1.055, while at 14,100 feet the specific gravity increased to 1.073. The general consensus of investigators is that the increase in number of red cells does not place an extraordinary burden on the circulatory system. In a study of chicks and the effect of supplemental vitamin E in hypoxia, the hematocrit at 4,900 feet was 34 percent and at 15,700 feet was 45 percent. The hemoglobin was

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40 mg/100ml and 50mg/100ml, respectively, when no supplemental vitamin E was given. Additional vitamin E had no effect on the hematocrit and hemoglobin at either altitude. However, the vitamin did have a significant effect on the production of immunocytes, which were greatly increased at altitude (248).

Hemoglobin varies with species (27, 55, 75). There appears to be a relationship between the classification of hemoglobin types (e.g. A, B, C) and the ability of the animal to adjust to or withstand hypoxic stress (27).

The anabolic hormone, metelone acetate, in combination with a B-vitamin complex produced a significant increase in erythrocytes, hematocrit, and hemoglobin when humans were subjected to a range of altitudes from sea level to 20,000 feet (5). Vitamin therapy with vitamins B_1, B_2, B_6, B_{12}, pantothenic acid, nicotinic acid and vitamin C was associated with insignificant changes in hematological values as compared to the combination with metelone acetate, but both treatments at all altitudes were significantly different from sea level hematological values during a 35-day experiment (5).

Hematological changes are significantly related to altitude and reflect the process of adaptation.

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Reynafarje reported the hematological values in natives of sea level and altitude shown in Table 1 (216).

Table 1

Blood Values of Sea Level and High Altitude Residents

Blood Component	Sea Level Native	High Altitude Native (14,100 ft.)
Hematocrit (%)	43.30 ± 2.50[a]	52.40 ± 2.55[b]
Hemoglobin (gm/100 cc)	14.41 ± 0.88	17.03 ± 0.89[b]
Myoglobin (mg/gm fresh tissue)	6.07 ± 0.70	7.03 ± 0.73[c]
Hemoglobin (mg/gm fresh tissue)	5.93 ± 2.44	9.58 ± 2.94[c]

[a]Mean ± standard deviation

[b]$P < 0.001$

[c]$P < 0.02$

Burton and co-workers have summarized the increases over sea-level values in hematocrit, hemoglobin concentration and erythrocyte count of man and three animal species adapted to high altitude, as shown in Table 2 (36). The results in Table 2 were interpreted as an indication that "the greatest and most consistent changes (in hypoxia) involve the oxygen-carrying capacity of the blood" (36). The authors also concluded that the primary erythrocytic response of the chicken is apparently a "net increase in total circulating red blood cells."

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Table 2

Percentage Change from Sea Level of Blood Values in Man and Three Animal Species at High Altitude

Blood Component	Man	Rat	Mouse	Chicken
	---------percentage increase---------			
Hematocrit	28	15	20	27
Hemoglobin	29	20	26	36
Erythrocyte count	26	25	22	33

The oxygen capacity, or the amount of oxygen the blood can actually contain if exposed to air, increases with the number of red blood cells. The increase in red cell count with altitude is an excellent measure of the concurrent increase in the oxygen-combining capacity of the blood (50, 70, 133).

The oxygen content, or the amount of oxygen actually present in the blood under a particular condition, is best measured with respect to oxygen capacity and is expressed as "percent saturation." The oxygen content declines with increased altitude, which is compensated for by an even greater increase in hemoglobin content of the blood (10, 87, 269).

The coagulation time of blood decreases with increased altitude, but the response is highly variable among species (269).

Hemolysis occurs only when the oxygen tension is greatly reduced, generally at altitudes above

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18,000 feet (269). Red blood cell fragility is of minor consideration below this altitude.

Leucocytosis, or an increase in the number of circulating white blood cells, occurs for only a short time immediately after exposure to high altitude. However, the proportion of the various types of white blood cells, i.e. the differential count, shows considerable variation both among and within species. For example, the polymorphonuclear cells may decline in favor of large lymphocytes in animals, but not necessarily in man (139).

It is evident that the body reacts immediately upon exposure to hypoxia, a response which attempts to provide more oxygen to the tissues by rapidly increasing the oxygen binding and transport systems.

Heart

The heart is a primary organ that responds to low partial pressures of oxygen. Its role is to increase the flow of blood to the tissues to an extent that will maintain a supply of oxygen adequate for tissue metabolism.

Cardiac Hypertrophy: The occurrence of cardiac hypertrophy is a significant physiological response to hypoxia (269). It is observed in species resident but not native to high altitude for periods of six months or longer,

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or longer, and in natives of high altitude (141, 252, 269). In hypoxia, cardiac hypertrophy is significant only if the degree and/or the duration is considerable (252, 269). Cardiomegaly is most often measured in two ways: (1) as the ratio of heart weight to body weight, or (2) as the ratio between the weights of the left ventricle and right ventricle. Gloster et al. have summarized the latter measurement in guinea pigs, rabbits and dogs as shown in Table 3 (99). The authors stated that these data support the observation that the increase in right ventricular size is greater than that for the left ventricle when these species are exposed to high altitude.

Table 3

Left and Right Ventricular Ratios on a Weight Basis of Three Species at Sea Level and 13,100 Feet

Species	Sea Level	13,100 Feet
Guinea Pigs	3.2	2.6[a]
Rabbits	3.5	1.9[a]
Dogs	3.3	2.2[b]

[a] $P < 0.01$

[b] $P < 0.05$

Badeer stated in a review of cardiac hypertrophy that right ventricular hypertrophy has been demonstrated in cattle, rabbits, lambs, pigs, guinea pigs, mice, horses, lla

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horses, llamas, chickens, pigeons and dogs native to high altitudes or after varying periods of acclimatization (10). Dogs native to sea level are resistant to cardiac hypertrophy when subjected to low barometric pressure. The neonatal chick native to high altitude shows a rapid increase in right ventricular size upon exposure to hypoxia (37).

In a study of rats at sea level, or pair-fed to high altitude intake or at high altitude, Gloster et al. showed that only high altitude conditions were associated with an increase in right ventricular size and lung weight (98). Cardiac hypertrophy occurs when dietary intake is reduced in hypoxia, but it is not known whether diet restriction accentuates or diminishes the hypertrophic response.

Van Liere has employed the measure of heart weight versus body weight in guinea pigs as a determinant for the occurrence of cardiac hypertrophy (259). He reported that the ratio increases 55.8 percent above the sea level value and varies with altitude above 12,250 feet. Valdivia determined that a progressive hypertrophy of the right ventricle occurs in guinea pigs which are exposed to a simulated altitude of 18,000 feet (257). This hypertrophy stabilizes after six weeks and no further enlargement occurs.

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In man, Kerwin (150) and Rotta (220) have used x-ray techniques to study the heart size of high altitude natives of Peru. They have measured an average increase in transverse heart diameter of from 11.5 to 21.3 percent over sea level controls.

Heart Rate: Changes in elevation of as little as 4,000 feet can cause a significant increase in heart rate in animals, but the rate is usually unchanged in humans (10). The mechanism of a change in heart rate is still not known, although most theories focus on the chemoreceptors of the carotid and aortic bodies as being instrumental in this response (269).

Cardiac Output: In anoxic hypoxia cardiac output increases rapidly in many species, then returns to near normal within a few days as blood hemoglobin increases. Although the mechanism is not fully understood, in 1940 Strughold (243) conducted the first convincing study that led to the current predominant hypothesis. It is thought that epinephrine and norepinephrine are liberated in acute hypoxia which cause an increased pulse rate, greater vasoconstriction and higher arterial pressure, which in turn cause the heart to beat more forcibly. In chronic hypoxia, no difference from sea level values of cardiac output has been noted in acclimated individuals (10, 269). Coronary blood flow also is increased in response to hypoxia.

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The respiratory rate increases in high altitude conditions, following even moderate exercise by unacclimatized individuals. Arterial saturation by oxygen declines, as do the partial pressures of alveolar oxygen and carbon dioxide. The minute volume, tidal volume and oxygen consumption all increase in hypoxia (213). Because of oxygen want the breathing patterns become abnormal, but tend to return to a less-abnormal state as the individual becomes acclimatized (269). Man resting at sea level has an oxygen requirement of about 350cm^3 per minute. At 11,300 feet the number of oxygen molecules per unit volume is reduced by one-third. The partial pressure of oxygen at the alveolar level is reduced from 96 mmHg to 64 mmHg (alveolar hypoxia). The diffusing capacity of the lung limits oxygen uptake per inspiration to about 20-25 percent of the total amount available. Hyperventilation occurs and increases the total oxygen inspired. Hypoxia exists when pulmonary oxygen is below body needs. Von Muralt suggests that the oxygen requirement at the tissue level should be the primary criterion for studies concerning the effects of diminished oxygen pressure and the compensatory responses of the body (274). The oxygen consumption at high altitude has been shown to increase 11 percent (67), and up to 32 percent (76), over sea level values.

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Pulmonary hypertension associated with cardiomegaly and cardiac failure is often observed in man, cattle, pigs and rabbits but is rarely seen in lambs and cats (10, 215). Bisgard et al. determined that calves do not hyperventilate during acclimatization to high altitude (21). As a result, calves are more hypoxic at altitude than is man who does hyperventilate (223). Among the breeds of the bovine species, the Holstein calf has a pulmonary bed which is highly reactive to acute and chronic hypoxia. This renders the breed more susceptible to right heart failure, and of all the bovines, it displays the poorest ability to adapt to high altitude.

Gastrointestinal Tract and Accessory Organs

Of the four distinct forms of hypoxia (anoxic, hemic, stagnant and histotoxic), it is the anoxic condition that has been most studied with respect to its effects on the alimentary tract. Anoxic hypoxia moderately reduces gastric motility in man (126) and dog (60). In the normal, trained dog, simulated altitudes above 18,000 feet produce a loss of gastric tone and a diminution in the strength of hunger contractions (261).

The effect of hypoxia on gastric emptying time in rats was demonstrated as an increase proportional to the degree of hypoxia and was not related to hypocapnia (reduced ca

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(reduced carbon dioxide in the blood) (58). In an earlier study an inhibition of gastric emptying time due to hypoxia could not be demonstrated (179).

In dogs, Van Liere and Stickney showed that the threshold for elevated gastric emptying time lies at 8,000 feet, under simulated altitude conditions (262). Again, the time required for the stomach to empty was proportional to the degree of hypoxia. This threshold and relationship has also been found to be characteristic of the response of man to hypoxia, although there is considerable variation among individuals (13.2 to 166.9 percent of the normal value for emptying time) (258). Another study has shown that the exposure of man to a simulated altitude of 12,500 feet or, to a true elevation of 15,000 feet, resulted in delayed gastric emptying times (231). The results of these studies suggest that the phenomenon should be studied further, since it may have a major effect on nutrient utilization.

The mechanisms of delayed gastric emptying time in the rat, dog and man can be summarized as follows: (1) the low oxygen partial pressure stimulates vagal innervation of the pyloric sphincter, which then contracts, and (2) severe hypoxia will then directly affect the gastric musculature. Both stages reflect oxygen want at the tissue level. Another mechanism has been suggested, supported by the investigations of Van Liere et al. (26

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et al. (264), Smith (236) and Wilder and Schultz (279). The hypothesis is that since epinephrine can delay gastric emptying time upon administration, the stimulation of secretion of this hormone by hypoxia should cause a similar effect on the stomach.

Under conditions of hemic hypoxia (low hemoglobin in the blood but normal levels of oxygen, best produced experimentally by bleeding up to 30 percent of the blood volume) there is an increase of gastric tone and hunger contractions (41) and a longer gastric emptying time (268).

Extensive investigations by Van Liere and his associates on rats and mice indicated that peristalsis or propulsive motility of the small intestine was inhibited at simulated altitudes of 18,000 feet and above (260, 266). Altitudes of 14,000 feet produced no significant inhibition of peristalsis over sea-level conditions.

It should be noted that before any significant effects of hypoxia on the gastrointestinal tract are detected, oxygen deficiency causes more severe changes in cardiac and cerebral function (201, 269). Compared with the central nervous system, the gastrointestinal tract is relatively resistant to the terrestrial hypoxias normally encountered (269).

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Hypoxia reduces gastric secretion in the dog and man. The pH of the secretion increases and the total acid in the gastric juice decreases in the dog at altitudes of 18,500 feet and above (208). The threshold for these changes in man appears to be about 13,000 feet, although the few studies that have been conducted have provided conflicting results (269).

The total volumes of pancreatic secretion, amylase, bicarbonate and trypsin are decreased in man subjected to simulated altitudes of 18,000 feet and higher (123). Only in severe hypoxia (equivalent to over 25,000 feet altitude) is the bile flow reduced, accompanied by a concomitant reduction in bile salt secretion in the dog (45, 228), rat (122) and rabbit (7). MacLachlan was unable to detect these changes in the rat (180). Bile flow and bile salt secretion in the dog were not reduced in a study reported by Tanturi and Ivy (246). The conflicting evidence suggests that changes in the gall bladder are minor during hypoxia. Another study noted that human bile flow is not reduced upon exposure to survivable hypoxia, however severe, unless the patient already has impaired liver function due to liver disease (149). A human in this condition can undergo further liver function inhibition upon exposure to even moderate hypoxia.

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There is no appreciable direct effect of exposure to simulated altitudes up to 27,000 feet on absorption of water by the stomach. Present knowledge suggests that water is indirectly dependent on active processes but secondary to the active transport of solute in hypoxia (232).

Most investigators agree that hypoxia has little or no effect on capillary permeability to fluid and protein within physiologic ranges of hypoxia. Only in the case of severe oxygen restriction does permeability appear to increase. This is in agreement with the discussion of amino acid absorption. Edema is not easily produced by a deficit of oxygen, especially in humans, because the capillaries are quite resistant to this condition (269).

The flow of lymph is stimulated by hypoxia and can accumulate in the thorax. However, edema produced strictly as a result of increased capillary permeability has not been clearly demonstrated, and the mechanism of action is not yet understood (269).

Kidney

In man and animals the urine volume is increased in mild hypoxia, or that of short duration, and decreases in severe hypoxia. The decrease is thought to result from an increase in the secretion of anti-diuretic hormone (269).

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An elevated excretion of urinary electrolytes such as sodium, potassium and bicarbonate is associated with anoxic hypoxia (269). This secretion reflects an attempt by the kidney to maintain homeostasis in response to the respiratory alkalosis produced by hypoxia. Concurrently, ammonia secretion is reduced while urine pH is elevated.

In a review of the electrolyte changes in man in acute hypoxia, Janoski et al. reported that the production of aldosterone was variable in similar conditions of hypoxia (146). According to the authors an increase in aldosterone is not compatible with their observed increases in serum potassium content and renal retention of potassium.

A prominent feature of the renal changes in the high altitude native during exposure to hypoxia is an increase in filtration fraction (the portion of the plasma which is filtered through the glomeruli of the kidney) (195). This is explained by an increased viscosity of the blood at altitude in contrast with the vasoconstriction in the kidney seen in pulmonary hypertension.

Endocrine Glands

The endocrine glands secrete hormones that stimulate or inhibit specific metabolic activities in other tissues or organs. A disturbance in the metabolism

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metabolism of the endocrine glands, such as hypoxia, can affect the metabolism of target tissues and organs.

Adrenal Gland: Severe and/or long exposure to hypoxia can produce functional alterations in the adrenal glands of the intact rat which are identical to those seen in adrenalectomized animals (96). The alterations can be relieved, and for the most part corrected, by adrenocortical hormone therapy. The work by Giragossintz and Sundstroem suggests that the adrenals can be irreversibly exhausted by severe hypoxia, due to cellular necrosis and hemorrhage (96).

Under conditions of hypoxia compatible with life, adrenal weight is increased significantly, which is observed primarily as an enlargement of the adrenal cortex (269). A transitory decrease in adrenal lipid (63) and a depletion in adrenal cholesterol (61, 249) is associated with anoxic hypoxia.

In man, 17-ketosteroid urinary excretion increases proportionally with altitude (210). Increased adrenal cortical secretion is evident in the rat, mouse and rabbit for the 17-hydroxycorticoids, but not so in man (119) or the dog (89).

The production and secretion of epinephrine and the other adrenal medullary hormones are stimulated by hypoxia (269). The stimulation is a result of the effect of oxygen deprivation on the sympathetic nervous system. A

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system. An early review stated that these hormones enable the organism to adjust to the stress of hypoxia by increasing the cardiac output, by mobilizing glucose from liver glycogen stores producing hyperglycemia and by enhancing glycolysis. To the contrary, recent studies have shown that glycogenesis increases and glycolysis is reduced. It appears that although the adrenal medullary hormones do increase glycolysis and glycogen mobilization, the net changes are in the direction of glycogen storage and reduced glycolysis.

In summary, although an increase occurs in the secretion of adrenal hormones beneficial to the need for increased homeostatic function while adjusting to hypoxic stress, the reason for the higher levels of cortical steroids and their action on the thymic system is not yet understood. The benefit of an increase in circulating mineralocorticoids is also not clearly understood, since their presence would counteract the need for increased electrolyte excretion in response to the respiratory alkalosis of anoxic hypoxia.

Anterior Pituitary: One effect of stress in the mammal under normal conditions is for the hypothalamus to secrete corticotrophin-releasing factor which in turn causes the release of adrenocorticotrophin by the anterior pituitary gland (222). This chain of events is

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events is observed also in hypoxia. Adrencorticotrophin is responsible for mediating the release into the circulation of the hormones of the adrenal cortex.

Gonads: In rats and humans there are moderate changes in the structure and decreases in the weights of the ovaries, uterus, testes, seminal vescicle and prostate gland (269). Periodic exposures of rats to altitudes of 25,500 feet can prevent spermatogenesis due to the degeneration of the germinal cells (108). This effect could not be ameliorated by gonadotrophic hormone therapy, suggesting that hypoxia acts directly on the testes (108).

Uterus: The uterus of the dog is extremely resistant to anoxic hypoxia. This suggests, in light of the information in the previous section, that the reproductive system elicits a wide variety of responses to hypoxia, with species differences being the dominant determinant (265). In a study by Hilton and Woodbury using rabbit uterine strips in vitro, a reduction of the normal response to oxytocin during hypoxia was demonstrated (130). Oxytocin is a polypeptide hormone produced by the posterior lobe of the pituitary gland. A decrease in the sensitivity of tissues to oxytocin may be relevant to studies of high altitude dairy productior

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production and reproduction, because the hormone stimulates uterine contraction and the excretion of milk from alveoli in the mammary gland.

Thyroid Gland: In anoxic hypoxia, thyroid function in rats was severely inhibited and exposures to simulated altitudes of 27,000 feet reduced protein-bound iodine to one-tenth of the level observed before exposure (271). This reflects a severe depression in iodine uptake. The disappearance of protein-bound iodine from the plasma was normal in rats at sea level. Van Middlesworth and Berry concluded that thyroid function was severely impaired (271).

Thyroid function is modified in rats which are native to high altitude compared with genetically similar counterparts at sea level (200). There is a reduction of iodine uptake and sensitivity of the thyroid gland to circulating thyroid stimulating hormone in rats acclimatized to high altitude. High plasma iodine is characteristic of high altitude natives, which may be related to the decreased renal clearance of iodine observed in man at altitude (200).

Pancreas: The pancreas secretes insulin which regulates blood glucose levels. A deficiency of insulin causes an increase in blood glucose and a decrease in liver glycogen. Exposure to hypoxia stimulates the secreti

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secretion of insulin in the dog (182, 183) and rabbit (83). Increased insulin should produce an increase in liver glycogen and hypoglycemia. The latter effect is not consistent with the hyperglycemia of high altitude exposure. This suggests that insulin may not be the main operative factor and that its increased secretion is not sufficient to cause hypoglycemia.

Heat Regulation and Hypoxia

Animals and man show a decline in body temperature upon ascent to true altitudes or in conditions of simulated altitude. The body temperature of rabbits has fallen when the animals are exposed to an altitude of 14,272 feet (16). Mice maintained at room temperature, but exposed to an hypoxia equivalent to 24,000 feet, showed a decline in rectal temperature of 2.5°C in five minutes and 4-6°C in 15-20 minutes (94). Rats have shown an even greater response to hypoxia (94). Guinea pigs and kittens demonstrate an ability to maintain body temperature under mild hypoxia and neutral ambient temperature. However, in mild hypoxia combined with a lower ambient temperature their body temperature falls dramatically and oxygen consumption rate shows a similar decline (129). In man, rectal temperature falls in hypoxia even with neutral ambient temperatures (277). Another feature in man is that shivering stops in hypoxia.

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hypoxia. It is suggested that this is due to increased heat loss through the skin, which is confirmed by a concurrent increase in skin temperatures (157, 277). In hypoxia and cold conditions, the ability of humans to regulate their heat production appears to be impaired as compared with cold sea level conditions (17). Hill suggests that the characteristic decrease in body temperature and oxygen consumption in hypoxia is not due to the specific effects of hypoxia, but to the general limitation in absorption of oxygen from the atmosphere (129). Perhaps there is also a specific impairment of heat regulation by the hypothalamus (129).

The larger species of animals, such as the sheep, dog, cat and man can withstand better the initial reduction in oxygen consumption in hypoxia combined with low temperatures than can the smaller animals (269). The environmental temperature plays an important role because the maintenance of body temperature is in part dependent upon oxygen consumption. When ambient temperatures are maintained near neutral, oxygen consumption does not decline until severe degrees of hypoxia are encountered. If animals are exposed to even mild degrees of acute hypoxia, under conditions of low ambient temperature, the oxygen consumption declines immediately. The basal metabolic rate is dependent upon body temperature, hence upon ambient temperatu

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temperature under normal oxygen levels, and is especially dependent in hypoxia (56, 269).

Central Nervous System

Several studies have examined the effects of hypoxia on the nervous system. It has been shown that cartilage can withstand several hours of total oxygen deprivation, whereas nerve fiber falters after only a few minutes of oxygen insufficiency (269).

There is a direct effect on vision when hypoxia is encountered. Afterimages persist longer (175), the light intensity threshold increases (93, 229), visual acuity decreases (18, 177) and peripheral vision is reduced (120).

The effects of hypoxia on hearing are less pronounced than in the other sensory systems (30). The threshold for hearing in Andean residents has been determined at six to eight decibels higher than in sea level counterparts (176). In chronic hypoxia progressing to severe hypoxia, hearing is the last sensory system to falter (269).

There have been few studies on taste and smell and the results are inconclusive. It is thought that there may be a slight impairment of taste and smell caused by local anemic hypoxia, but of no metabolic significance (269). Von Muralt stated that there is

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a decline in taste sensitivity during the first few days of exposure to moderate hypoxia (274). Because there is a depression of appetite in hypoxia, and because taste and smell play a role in appetite in normoxic conditions, these senses may be more important in food consumption at high altitude than presently assumed.

The thresholds for touch and patellar reflex decrease at altitude (170, 274). The sensitivity to pressure on the skin and the two-point threshold are slightly impaired (170).

There are few data on the effect of hypoxia on pain. The most conclusive study was performed by Bullard and Snyder using the rat, and a hibernator, the ground squirrel (34). The response of rats to thermal pain was decreased when the rats were exposed to an atmosphere of 7.5 percent oxygen and was abolished when breathing 5.0 percent oxygen. The response of the ground squirrel to thermal pain was not affected until the squirrel breathed 2.5 percent oxygen. Hibernating species are able to withstand a more severe hypoxia than nonhibernating species.

In the chick embryo hypoxia has a major effect on brain development (233). The embryonic brain will develop normally at 10,100 feet but does not complete the early developmental stage during maturation at 12,500 feet elevation.

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Nutrition During Exposure to Hypoxia

There are few nutritional studies of animals of economic importance under high altitude conditions. Data from low altitude research often disagree with the results of studies of man or laboratory animals at high altitude. Therefore, a review of studies having nutritional aspects potentially relevant to livestock is useful.

Anorexia or loss of apetite is one of the first and most pronounced problems of hypoxia facing the nutritionist. Anorexia, or the more frequently encountered diminished appetite, cause many of the maintenance and production problems observed in high altitude studies of animals or man. Many studies which have focused on physiological measurements during high altitude exposure have been complicated by the abnormal nutritional status of their subjects during the trial (269). For example, in a study of physiological changes in rats kept at a simulated altitude of 28,000 feet for only three weeks, the rats lost 20 percent of their body weight (154, 167). In another study using men at an altitude of 17,000 feet for twenty-six days, there was an average weight loss of eleven pounds (211). Above a critical altitude animals will not eat. This altitude varies with species (17, 39).

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The obvious result of decreased appetite is reduced food consumption, which ultimately can lead to reduced body weight gains in growing animals or man, or a loss of body weight in mature organisms, usually during the initial weeks of exposure. This point was illustrated in a study of troops stationed in Colorado at 9,000 feet and training from 10,000-13,000 feet of altitude (112). At the end of thirty days the men were consuming 3,750 calories daily. After two months their caloric intake had increased by only 120 calories per day. However, after a period of three and one-half months, sufficient for substantial acclimatization to occur, the daily caloric intake had risen to 5,000 or an increase of 1,250 calories above the control level.

An interesting aspect of appetite during hypoxia is a voluntary change in preference for various foods. In the beginning of the above study the men consumed 39.8 percent of their diet in the form of carbohydrates and 46.9 percent as fat (112). After three and one-half months of acclimatization, the percentage of carbohydrates in the diet increased to 44.1 percent, while the proportion of the diet as fat declined to 43.4 percent. The relationship of hypoxia to diet preference has been documented in many reports of mountain climbing expeditions. Information from three of them serve to illustrate the relationship.

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At altitudes greater than 21,000 feet the appetite decreases initially as has been noted above. However, in addition to a general loss of appetite, there is a distinct dislike for solids such as meat, and a pronounced desire for sweets, soups and fruits (131), jams and chocolates (176) and pineapple cubes and tinned salmon (211). In the latter case the items were not available on the expedition and rather than eat food that did not appeal to them, some men refused to eat anything. High protein diets are poorly tolerated at altitude. Rats often lose weight when they are exposed to hypoxia, even while consuming a diet adequate in protein to sustain maximum growth at sea level (154).

Many studies have supported the observation that hypoxia is associated with a loss of body weight (39, 49, 54, 56, 97, 167, 211, 245, 278). Klain and Hannon stated that the decline in sustained body weight in man and the decreased growth rate in laboratory animals under hypoxic conditions are apparently due to: (1) anorexia, as a result of a voluntary decreased caloric intake; (2) a concomitant decrease in the efficiency of food utilization; and (3) altered gastrointestinal tract function (154).

A recent study of rats by Gloster et al. demonstrated a definite effect of hypoxia on growth (97). The study included both weanling and mature rats fed

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rats fed the same diet but exposed to two barometric pressures and three feeding schemes. The first treatment was *ad libitum* feeding at sea level pressure. Treatment two included rats fed the diet *ad libitum*, but at a simulated altitude of 18,000 feet. The third group was maintained at sea level pressure, but was pair-fed to the intake of the high altitude group. A summary of the data is presented in Table 4.

Table 4

Body Weight Gains and Feed Intakes of Rats Subjected to Two Altitudes and Three Feeding Schemes

Animals	Treatment		
	1	2	3
Weanling rats	81 (13.2)[a]	41 (8.8)	37 (8.4)
Mature rats	58 (27.7)	-2 (16.9)	21 (17.8)

[a]Grams of body weight gain (feed intake, gms/day)

Based on these results, the authors concluded that high altitude affected body weight gain and intake more severely in mature rats than in weanling rats.

Reduced food intake in conditions of high altitude may not be the only factor operative in lowered body weight gain. This was especially evident from the body weight loss of mature rats in treatment two. The study by Gloster et al. included a careful examination of the organs of the rats (97). Both age groups had

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significantly ($P < .05$) smaller liver and kidneys in treatments two and three. Hypoxia exerted a direct effect on kidney size, whereas diet restriction appeared to be the operative factor in reduced liver size. There was no difference in heart weight between groups two and three, although there was a significant difference ($P < .05$) in body weight between treatments two and three at the end of the trial. The right ventricular weight was significantly ($P < .05$) greater for both ages of rats exposed to high altitude than those at sea level. In general, diet, or food intake, is the most important factor affecting body and organ weights and is aggravated by hypoxia. The water content of the above organs was unaffected by any of the variables. The authors concluded that the diminished intake of food due to anorexia at high altitude can account for most of the reduction in body weight and growth rate.

Adult humans were offered a normal diet, or a high carbohydrate diet with low fat content, in an eight-day adjustment period at sea level, during a stay of twelve days at 14,100 feet and during a seven-day recovery period at sea level (57, 158). The total calories of the normal diet were composed of 48 percent carbohydrate and 40 percent fat. The high carbohydrate diet consisted of 68 percent carbohydrate and 20 percent fat. The duration of work on a treadmill was more than double f

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double for the high carbohydrate diet at altitude. The total calories offered were 3,600 per day. Table 5 presents the changes noted after twelve days at altitude.

Table 5

Changes in Body Composition and Caloric Intake at High Altitude

Measurement	Normal Diet	High Carbohydrate Diet
Change from control period (kg):		
Body weight (total)	-3.54	-3.96
Body fat	-1.29	-1.46
Body water	-1.77	-1.85
Dry body protein	-0.32	-0.47
Body mineral	-0.16	-0.18
Daily caloric intake (Kcal):		
Control (8 days)	3070	3160
High altitude (12 days)	2130	1920
Recovery (7 days)	2680	2540

The authors concluded that body weight lost in excess of that attributable to the caloric deficit was due to a loss of body water. That the blood and plasma volumes were significantly lower at altitude indicated a hypohydration of the body.

The efficiency of food utilization by rats fed *ad libitum* at 14,100 feet of altitude was only 60 percent of that observed at 5,280 feet (49). The significantly lower food efficiency suggested that there was much potentia

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potentially utilizable energy being lost in the feces due to hypoxia, which impaired both digestion and intestinal absorption. Rats at high altitude ate less food yet excreted more feces, indicating there was a decrease in apparent digestion or a decrease in metabolizable energy absorbed by the gut.

The chick embryo is susceptible to the effects of hypoxia, mainly in the form of repressed metabolism, which resembles the effects induced by moderate hypothermia (233). The most serious effect of hypoxia in the chick embryo is a high mortality rate during incubation. Embryonic growth, the differentiation rate and the respiratory rate are all slowed, and the latter is the most susceptible to reduced oxygen tension.

The epidermal and intestinal microbial flora of man are not affected by his environment at sea level or high altitude (276). Conversely, the response of man to hypoxia (e.g. increased hematocrit and hemoglobin) is not affected by his microbial flora.

Dysfunction During Hypoxia

The exposure of man and animals to either acute or chronic hypoxia can produce general systemic dysfunction in addition to the variety of specific alterations discussed above. The symptomatology of the dysfunct

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dysfunction is similar in man and animals, and relief usually is possible only upon descent to lower altitudes.

Brisket Disease

Brisket disease is an epizootic disease of cattle and is diagnosed as a heart condition which occurs in high mountain areas. The accumulation of fluid in cattle causes a swelling of the brisket, neck and lower jaw and is a prominent feature of severe circulatory disturbance. Hecht et al. stated that the redistribution of fluid in brisket disease is clearly a manifestation of right-heart failure brought on by pulmonary hypertension as a result of altitude (125). In cattle, the blood vessels going to the lungs constrict because of the low oxygen, causing the heart to overwork. The right side of the heart enlarges, due partly to reduced oxygen, which increases the work load of the right ventricle (22). As a result, circulatory failure occurs and body fluids become imbalanced. In many cases of circulatory failure at altitude swelling of the brisket is not evident, but when it occurs it is more often seen in young animals than in adults. Whenever the swelling is not observed, yet the animal dies and upon autopsy has signs similar to those of brisket disease, the right side of the heart has enlarged so rapidly that the heart failure occurred

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before circulatory disturbances became extensive. In Utah, 75 percent of the cattle with brisket disease have external signs of fluid imbalance (22).

The most extensive studies of brisket disease have been conducted since 1915 in Colorado and Utah (22, 24, 100, 101, 102, 124, 125). In Utah, the disease rarely occurs below 7,000 feet of altitude and appears sporadically above this elevation (24). It has been known since 1889 to occur in Colorado (100).

The symptomatology of the disorder is similar, in some respects, to cardio-respiratory disturbances in man. Brisket disease is clearly altitude-related, whereas in man cardio-respiratory problems can occur at sea level as well as at altitude (124, 125). Brisket disease generally occurs at altitudes well below those necessary to cause disturbances in man, and the physiological signs are more severe for cattle than for man at the same altitude. The maladaptation syndromes are interrelated in both species. In man, it is seen as a severe hypoxia and polycythemic response; in cattle, as pulmonary hypertension and heart failure (124, 125).

Circulatory disturbances include the leakage through vessel walls of fluids which accumulate between the cells of various tissues. This condition is called edema and is most evident in the brisket in cattle, under th

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under the lower jaw, and in the tissues supporting the kidney, the intestines and the lungs (22). The fluid can pool in the thoracic cavity, abdominal cavity, and in the cardiac sac.

In addition to edema the principal characteristics of the disease in cattle include dyspnea (abnormally heavy breathing), cyanosis of the mucous membranes, prostration, rough fur coat and a visible jugular vein pulse (125). In Utah, 82 percent of new cases of the disease show a distended jugular vein in the form of wave-like pulsing with each heart beat (22). This is due to an incomplete closure of the heart valves between the right atrium and right ventricle, which results in a backward flow of venous blood. Usually, body temperature is not elevated unless a secondary disease develops. Diarrhea, although common, and lesions of the mouth, observed less often, are not diagnostic of the disease.

Both pulmonary diseases and liver flukes can produce symptoms similar to those of brisket disease, especially cardiac hypertrophy and edema. Unfortunately, certain diagnosis can be made only upon post-mortem examination (22).

The incidence of brisket disease is greatest in areas comprised of subalpine plateaus having either a few large swamps or many small scattered swamps and

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seep holes (24, 125). It is thought that moist and marshy pastures combined with high altitude cause brisket disease due to excessive fluid and salt intake which results in heart failure (125). Excessive salt intake has been observed in grazing steers given free-choice minerals in high mountain areas (124). In Utah, the disease rarely occurs in high mountain areas having rough terrain and little moisture, which are associated with vegetation dominated by browse type plants (24). The dominant plants of three distinct areas are: (1) rushes and sedges found in the marshy plateaus; (2) sedges and grasses in the gently-sloping area (the transition zone); and (3) grasses and brush on the higher, steeper slopes. Cattle prefer the vegetation of the swampy and transitional areas over the browse type of grasses and brush on the higher slopes. The wet meadowland forage is deficient in calcium, cobalt and possibly magnesium, while there is often an excess of potassium (24). Affected animals often are marginally anemic (23).

The incidence of the disease is highly correlated with the wetness of the grazed area and may reach as high as 5 percent even with good management practices (24). Up to 2 percent of the cattle grazing the transitional areas can be affected. The incidence depends on the year and climatic conditions, and the severity is

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severity is proportional in all grazing areas. An unusually high incidence of the disease in the worst areas can be as much as 10 percent of the animals grazing there, accompanied by an abnormally high incidence in even the best of pastures.

In cow-calf grazing operations the disease occurs twice as often in calves under one year of age as in the cows (6, 24, 125). The incidence in adult males and females is approximately the same. However, of the cases which occurred in calves approximately two-thirds involved steers. No data are available on the effects of noncastration on the incidence. The sex ratio of bovines at high altitude was reported to be 51 percent females to 49 percent males (24). Herds of cattle native to high mountain areas may experience a 2 percent death loss due to brisket disease, whereas the cattle in herds brought from lower areas may suffer a death loss of up to 40 percent (6).

The effect of season on the occurrence of brisket disease is significant in Utah (24). Approximately 84 percent of the cases in a six-year study occurred during the trimester from August through October, with half of them appearing in September. Over 93 percent of all the cases occurred from July through November, which coincided with the summer grazing period.

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The treatment of brisket disease with any assurance of success is difficult because the disease is not fully understood. The difficulty of treatment is further complicated because the heart is often damaged beyond repair, the lesions are always severe, the physiological stresses are great, and affected animals are usually in an advanced condition when the disease is discovered (23).

An extensive study of several treatments which were designed to remedy the major symptoms of brisket disease was conducted in Utah (23). The diuretics benzydroflumethiazide and chlorothiazide were used to correct the body swelling (edema and free fluid pools). The former drug was generally effective in reducing swelling when administered every other day for six days at 1.0 to 1.5 grams per 1,000 pounds body weight, but was less effective in reducing the overall severity of the disease. Chlorothiazide effectively reduced swelling when administered either orally or intramuscularly but is expensive. Cardiac glycosides (deslanoside and acetyldigitoxin) were effective in restoring the rhythm and magnitude of myocardial contractions of the enlarged heart. A preliminary examination of the hypertensive drugs reserpine, mebutamate and triamcinolone acetonide indicated that they were ineffective in ameliorating the symptoms of

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The Utah study led to the development of management recommendations which include the use of diuretics, digitalis, electrolyte mixtures to restore acid-base imbalance, anti-hypertensive drugs and tranquilizers, and the tapping and draining of the edematous areas (23).

Cattle suffered from brisket disease after having been moved from near sea level to 11,500 feet (250). Edema formed in the brisket area and spread to the flank and other body cavity areas. These are classic symptoms of the disease. The edema was temporarily relieved by tapping and draining the edematous regions. However, this remedy does not treat the causes of the problem, only the symptoms. Additionally, no success was achieved in reducing the edema by the use of purgatives. One-third of the animals died within eight to fifteen days after reaching high altitude. Young and adult animals were equally affected. It was suspected that cold temperatures as well as the great change of altitude caused the deaths.

Because animals of the same breed respond differently to the stresses of high altitude, it was suggested that there may be a genetic difference which has a role in the development of resistance to hypoxia (125).

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Several herds grazing in the same area are often affected to different degrees. In addition, animals within the same breed raised at high altitude are better able to stand the rigors of high mountain grazing. In 1965, a study was reported on six generations of cattle from a herd that had been affected with brisket disease (6). The foundation stock had been transported to a lower elevation after showing signs of the disease at high altitude and was then studied for six generations. Another group was selected from animals unaffected by high altitude and was maintained for six generations under high altitude conditions. The ancestors of the resistant stock had no history of brisket disease and also had low pulmonary arterial pressure even at high altitude. The offspring of the susceptible group maintained a high tendency to contract the disease. In contrast, the incidence was very low in succeeding generations of the resistant stock. While the authors concluded that the evidence is substantial that resistance is inherited, the particular traits which provide the resistance are not known. They stated that there appear to be two possible reasons for cattle having a higher susceptibility to brisket disease: (1) the animals have more reactive lung vessels, or (2) overall respiratory patterns are different. The data of Hecht et al. agree with this reasoning because they sugges

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they suggest strongly that cattle, compared with other species, have an excessive development of their pulmonary artery musculature which results in an excessive vasoconstrictive response to hypoxic conditions (124).

In addition to elevated hemoglobin levels in calves at high altitude, the animals suffering from brisket disease have an even higher hemoglobin level than those unaffected. This would support the hypotheses which suggest there is an interference with oxygen availability at the pulmonary level (124, 215).

The excessive pulmonary reactivity of cattle breeds of European origin to hypoxic conditions does not exist in other cattle breeds or in other ruminants (124). The buffalo, zebu (*Bos indicus*), yak, llama, alpaca and vicuña apparently are able to adjust sufficiently to hypoxia through a variety of specialized mechanisms.

Early attempts to learn more about brisket disease eliminated some factors from later consideration (101, 102). That the disease may be contagious was disproven by experiments in which the blood from affected animals was transfused into normal stock. There was no development of brisket disease. In an attempt to eliminate the possibility that the forage of high altitude caused brisket disease, native forage was fed to cattle at lower altitudes. None of the animals wer

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animals were affected. However, these studies do not preclude the possibility that nutritively balanced rations may aid in reducing the severity of the disease, and perhaps in its prevention. Studies of short duration also may not elicit the true effects of diet at high altitude. As indicated earlier, nutrition may play an integral role in avoiding or reducing the debilitating effects of high altitude, primarily by the provision of sufficient energy and proper electrolyte balance. To this extent, the synergistic effect of diet and altitude may be more important than presently assumed.

Management recommendations either to save the affected cattle or to minimize the severity of the disease include moving the animals to an altitude below 5,000 feet, limiting water and salt intake, and providing a well-balanced ration of high quality alfalfa hay and trace minerals (24).

Mountain Sickness

The illustrative account by Fray De Acosta in 1589 described the effects of short-term exposure to high altitude (147). The discomfort can be severe and debilitating. There is a major chronic dysfunction, however, during long exposure to high altitudes, generally referred to as mountain sickness, mountain disease, altitude sickness, high-altitude disease or

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Monge's disease. This terminology refers to human maladies, contrasted with the brisket disease of cattle, and has been most thoroughly described by C. Monge C. and C. Monge M. as a result of investigations in Peru (193, 194, 196, 197). In its greatest severity the sickness can cause death. There are many people born and raised at high altitude who do not survive the conditions and either die or develop and perform poorly, depending upon the degree of the disease. Many persons with severe forms of the condition will recover satisfactorily upon descent to a much lower altitude. Individuals who reside for great lengths of time at altitude are also affected in varying degrees. Those who suffer from the disease after long exposure are unable to adjust to the conditions and do not perform satisfactorily. They suffer nausea, vomiting, headaches, mental and physical depression and gastrointestinal disturbances (269). Specific information on mortality due to high altitude-related stress may be due to the lack of precise knowledge of the disease and the absence of adequate diagnostic techniques.

Monge proposed that high altitude sickness is a loss of natural acclimatization (194, 196). It is characterized by an abnormal metabolic hypoxia, with hypoxic responses greater than those measured in persons not suffering from altitude sickness. This includes

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an increase in red blood cell count above that measured for the altitude, an exaggerated increase in blood volume, greatly increased erythropoietic activity, abnormal cardiac hypertrophy, greatly accelerated cardiac output and a very low peripheral blood pressure.

Monge's disease in Peru has been described by several authors. However, there is no reported description of a similar disease in the Himalayas (158, 159). Lahiri did not encounter any cases of the disease during several visits to that area (159). Hemoglobin concentrations were normal in 200 individuals living at 15,000 feet of altitude. In contrast, the hemoglobin concentration is unusually high in natives of the Andes in Peru at similar altitudes. Lahiri stated that the difference between Himalayan and Andean populations could be related to differences in something other than altitude such as genetic history, diet or environment, and that Monge's disease may not be primarily a disease of chronic hypoxia. Milledge suggested that one difference may be the climate, because the Himalayas have a dry climate most of the time but Peru at altitude is damp much of the time (188). This generalization is not completely valid because there are many dry areas at high altitude in Peru, especially in the southern half of the country.

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Acclimatization and Resistance to Hypoxia

The acclimatization of man and animals to hypoxic stress has been described by various authors. The general consensus of investigators is that overall metabolism is most affected during the first hours and days of exposure, although many of the slower metabolic processes continue to change as exposure proceeds. The metabolic processes most critical to maintain life undergo the greatest changes upon initial exposure. The general response of the body is to maintain a homeostasis which will not drastically alter the normal functions of work, growth or maintenance (242, 269).

Acclimatization

Van Liere and Stickney have suggested that complete acclimatization occurs when the organism sustains: normal body weight gains when young, maintenance of body weight in adults, no loss of appetite, normal fertility and a feeling of general well-being (269). One known problem with these criteria is that for the newcomer to high altitude such conditions are difficult to achieve and are rarely all operative in the person native to altitude. The concept of "normality" should be replaced by "acceptability" until norms for high altitude performance are established. It has been shown that even after full acclimatization to altitude t

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altitude the individual does not function as efficiently as during pre-exposure periods. To expect otherwise ignores the existence of high altitude as a significant stress. Acclimatized individuals are able to perform at acceptable levels, but often not at normal or sea level rates. Acclimatization is more related to survival and less related to efficiency.

Hurtado has described two main categories of acclimatization to high altitude (140). The first category operates along the entire partial pressure of oxygen gradient, from the inspired air to mixed venous blood. At sea level this gradient is a net change in oxygen partial pressure of 150 mm Hg, and a change of 49 mm Hg at 14,900 feet altitude. The second category is operative at the tissue level and results in an enlarged capillary bed and a modification of various chemical and enzymatic processes of internal respiration.

The reduction of the partial pressure of oxygen gradient, which signifies an adaptation to hypoxia, is due to the following:

1. Pulmonary ventilation (hyperventilation) increases 20 percent at 14,900 feet. At this altitude or at sea level the basal and resting metabolic rates are the same with respect to body mass.

2. A decrease occurs in the alveolo-arterio gradient for oxygen. The oxygen-diffusing capacity is greater in acclimatized residents of high altitude.

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3. Polycythemia, accompanied by elevated hematocrit and hemoglobin levels, results in an increase in oxygen content at a given blood volume despite the decline in hemoglobin saturation by oxygen. Polycythemia also helps to minimize the effects of the decline in the oxygen gradient from arterial to venous blood, and increases the buffering capacity of the blood for carbon dioxide. Increased erythropoietic activity is accompanied by a more rapid plasma and red cell turnover, and a higher rate of iron utilization.

4. The cause of the changed affinity of hemoglobin for oxygen has not been well established. It is known that the partial pressure of carbon dioxide declines as a result of hyperventilation, which is compensated for by a proportional decrease in blood bicarbonate. However, the total buffering capacity of the blood is reduced, thus diminishing its ability to maintain an adequate acid-base balance (140).

Compared with the sea-level resident, the high-altitude native or acclimatized resident under the stress of exercise at sea level has:

1. A greater tolerance to maximal exercise;
2. A greater oxygen efficiency for the accomplishment of physical tasks;
3. A lower pulse rate and a smaller variation in peripheral blood pressures;
4. Less acidosis due to decreased production of lactate and pyruvate;
5. A lower oxygen debt.

Hurtado summarizes by stating that work capacity is perhaps the best index of altitude acclimatization (140).

Both physically conditioned and unconditioned altitude residents have a higher aerobic capacity than newcomers to altitude (186). Altitude residents compare well with

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well with partially acclimatized athletes. The high degree of fitness of rural Andean Indians derives from a lifetime of conditioning and acclimatization.

Andean children are significantly underweight compared with sea level children of similar racial background (138). Newcomers to Peru lost weight initially and never regained their sea level weight, even after a substantial acclimatization period (15). The initial weight loss is explained as follows: an initial decline in appetite and disturbances in the gastrointestinal tract lead to a loss of good, sound sleep. These factors, combined with labored breathing after exertion and a reduction in cellular oxidation, create a continued metabolic stress (269).

The process of acclimatization to chronic hypoxia is characterized by adaptations summarized by Van Liere and Stickney:

1. The most prominent respiratory feature is the almost immediate hyperventilation which develops. Hyperventilation elevates the pulmonary oxygen tension, and simultaneously reduces alveolar carbon dioxide tension. The adaptation is complete for the given conditions when blood pH falls within the normal sea-level range, as a consequence of an adequate reduction of alkaline reserve.

2. The adrenal cortex plays its role in the initial acute phase of hypoxia, both during the period of adjustment of acid-base balance and as the demands on carbohydrate metabolism are increased.

3. A minimum degree of right-heart hypertrophy follows an initial increase in cardiac output, which returns to pre-exposure levels after adaptation.

4. In most tissues a great increase in vascularity occurs, which vastly improves the diffusion of oxygen, metabolites and nutrients to the tissues.

5. The oxygen-carrying capacity of the blood increases greatly. There is an increase in the oxygen tension in the tissues that reflects a greater release of oxygen from the hemoglobin. This is due either to an actual reduced affinity of the hemoglobin for oxygen, or to lower blood pH, or both.

6. The plasma volume does not increase. The observed elevation of total oxygen-carrying capacity is substantially related to the increase in blood volume or polycythemia. The hypoxic polycythemia is the result of increased red blood cell formation and destruction, the equilibrium favoring the former. The life of the red cell remains unchanged. The increased red cell turnover is associated with the bilirubinemia observed in individuals acclimatized to high altitudes.

7. There is no evidence that the resting metabolic rate changes in hypoxic conditions.

8. Growth and body weight remain normal.

9. Some evidence suggests that the capacity for work is the same in an acclimatized individual as at sea level. More work is needed on this subject.

10. There appear to be some changes in renal physiology in hypoxia but these do not prevent effective kidney function in acclimatized man.

11. Based on incomplete evidence the gastrointestinal tract appears to maintain normal function. Greatly increased gastric emptying times occur only during the acute hypoxic phase of acclimatization.

12. The accumulated evidence on acclimated man indicates that fertility and reproduction are normal.

13. Reduced reaction times and increased auditory thresholds indicate that hypoxia can affect the nervous system (269).

The above summary, although extensive, includes only physiological changes. An exhaustive search of the literature has revealed a dismal paucity of high altitude research focused on those species of animals which are of economic benefit to man. Most of the research has been conducted under dietarily controlled, simulated altitude conditions, by physiologists who have contributed greatly to the store of knowledge related to circulatory and respiratory phenomena. However, the summary provided by Van Liere and Stickney reflects the lack of information on the role of nutrition in high altitude phenomena. For example, item number three implies that hypertrophy is only a minimal change during adaptation. However, in animals, right-heart hypertrophy is a major adaptive change and can be so extensive as to cause death in cattle (22, 23, 24, 144, 145). Enlarged livers are also a common finding in cattle living at altitudes as low as 7,500 feet. Point number eight ignores the data on livestock grazing at high altitudes, in which weight gain is often so marginal as to prohibit exploitation of the area for economic reasons. This situation is basically a nutritional problem, as well as physiological, because the forages encountered at high altitude grow slowly and are often of poor nutritional quality. In point eleven, almost all of the evidence is physiological. Certainly there are known characteristics of feeds, such as density, particle size, texture, fiber content and the content of other nutrients, which affect gastric emptying time, motility and other gastrointestinal functions near sea level. Unfortunately the gastrointestinal response to these feed characteristics during exposure to the hypoxia of high altitude is not known. Point number twelve suggests that reproduction in animals is normal. Yet, it is known that the poor reproductive performance of livestock in Ecuador, especially at altitude, is a major economic problem (144, 145).

Resistance to Hypoxia

There have been several attempts to increase the resistance of animals to the effects of hypoxia. Much of the therapy has involved hormones and biological chemicals, as well as surgical preparations designed to elicit those metabolic pathways that are operative in response to the stress of hypoxia. Almost all of the studies have guaged the resistance of animals to hypoxia by measuring either the survival time of animals under identical hypobaric conditions, or survival, as a function of the ability of the animal to withstand differing degrees of hypoxia. The following hormone

therapy has been shown to increase resistance to hypoxia: adrenocorticotrophin (ACTH) in rats (166); cortisone in guinea pigs (237); adrenalin (95) and diethylstilbesterol in rats (66). Hormones which decrease hypoxic tolerance include: thyroid stimulating hormone (TSH) (221), thyroxine (162), and insulin (230). Progesterone (79), testosterone (66) and diethylstilbesterol (104) had no effect on resistance.

The removal of various endocrine glands has shown that thyroidectomy increased resistance (13, 162), while adrenalectomy (166) and hypophysectomy (256) reduced resistance.

Several conditions have an effect on resistance to hypoxia. An increase in resistance is observed in hypothyroidism (281); fasting of long duration (160, 163, 234); in rats (205, 206, 212) and mice (206) exposed to excess humidity; excess carbohydrate intake (59, 113, 127, 218); and hypothermia in rats (52, 64, 143, 219), in mice (2, 128, 157), in guinea pigs (189, 191), in ground squirrels (33), in puppies (190) and in mature dogs (157). Decreased resistance is seen in fasting of short duration, less than twenty-four hours, in rats (160, 163); hyperthermia in the rat (143) and guinea pig (189); and in the metabolic disorder hyperthyroidism (281).

A variety of inorganic and biological compounds have been shown to increase resistance to hypoxia in some circumstances: amphetamines (a transient increase in resistance) in aviators (71) and rats (151); diphenylhydantoin (Sodium Dilantin) (78, 106, 132); alcohol in narcotic doses (79); ammonium chloride in man (11, 12) and dogs (103); thiourea (104, 162); thiouracil (104, 106, 107, 137); nicotinic acid in rats (38); vitamin B_1 in rats (46, 47, 117); dinitrophenol (162); and carbon dioxide (48, 153, 155, 156, 213). Cobalt chloride administration at sea level produces polycythemia, and when used at high altitude polycythemia occurs to an extent which is beneficial in withstanding hypoxic stress (73, 263). When vitamin E deficiency exists in an animal its resistance to hypoxia is lowered. Upon tocopherol administration the resistance is increased above normal levels (134, 247).

Some chemicals have been shown to be of little benefit in resistance to hypoxia and some are detrimental. No benefit has been shown from the use of caffeine (79) or the enzyme inhibitor di-isopropylphosphate (DFP) (90). The effects on resistance from chlorpromazine and cytochrome C therapy are variable (269). Definite decreases in resistance have been reported for cocaine (169) and sodium bicarbonate (185). Survival time appears to be related to brain levels of adenosine triphosphate (224). The drugs acetazolamide, phenformin and ergotamine are moderately effective in reducing the discomfort symptoms of acute mountain sickness but have no significant effect on the improvement of performance at altitude (42).

The ability to withstand hypoxia can be enhanced by a variety of treatments which are beneficial to varying degrees. Those treatments which are beneficial affect either one or a combination of metabolic processes. Major treatments focus on the reduction of the metabolic rate by decreasing cellular oxidation, counteracting the alkalosis of hypoxia and decreasing the oxygen consumption. The most beneficial means of combating hypoxic stress without resorting to therapeutic measures is for the subject to spend a period of two to three weeks at an altitude intermediate to the anticipated final altitude, whether the ascent be for purposes of recreation or work, or for production in the case of animals (172).

The young of several species can withstand hypoxia to a greater degree than the adults (81). In a study by Fazekas et al. which is representative of the results of many studies, the newborn of the rat, dog, cat, rabbit and guinea pig were variably more tolerant of hypoxia (81). The young of the rat and dog were more tolerant of hypoxia because of poikilothermia, the ability to greatly reduce body temperature in order to diminish metabolic demands. DeHaan and Field stated that a possible explanation of the resistance of the young of several species to hypoxia was, in part, due to their high glycogen levels and their ability to metabolize lactic acid and pyruvic acid to lipids (68). The principal exception to the response of the young is found in the bovine. A series of studies in the past sixty years has focused on the several breeds of cattle and their production at high altitude (100, 101, 102, 124, 125, 144, 145, 253). These studies have demonstrated the susceptibility of cattle to hypoxic stress, and the inability of the young to survive as well as the adults.

Jordan (148) makes an interesting speculation that perhaps the metabolic rate changes that are observed after ascent to altitude are related not to alterations in oxygen partial pressure, but are instead a result of a decrease of nitrogen narcosis. It can be considered that we are living under an obviously tolerable nitrogen narcosis at sea level. It is known that under normoxic conditions a decrease in nitrogen will increase the metabolic rate. This is an interesting hypothesis and warrants further study.

Summary

The review of literature has focused on the major physiologic and metabolic changes known to occur in man and animals when they are exposed to an environment having a reduced partial pressure of oxygen. Most research conducted in the past 100 years on high altitude phenomena has focused on physiological changes. Some studies have investigated nutritional aspects of hypoxia. However, there were few studies which examined the effects of nutritional status on the responses to high altitude in livestock of economic importance.

The major physiological responses to hypoxia provide increased transport capacity for oxygen in the blood. Hyperventilation partially compensates for the lower oxygen tension in the inspired air. Heart rate and size increase to circulate more blood. Hemoglobin levels increase while the affinity of hemoglobin for oxygen decreases, thus facilitating its release to the tissues. The number of red blood cells is elevated as a consequence of increased erythropoiesis in the bone marrow. Transient increases of circulating red blood cells are produced by the release of erythrocyte reserves from the spleen. The kidney regulates the alkalosis resulting from hyperventilation by increasing bicarbonate excretion. All of these changes occur during exposure to hypoxia, resulting in an increase in the oxygen content of the blood above sea level values, but the mechanisms are subject to controversy. The extent to which they occur determines, in great part, the ability of the organism to maintain normal productive and reproductive functions.

The present knowledge of the changes of tissue constituents as a result of exposure to hypoxia is derived from a limited number of studies. There is a general consensus among investigators that increases occur in glycogenesis, glucose tolerance, fatty acid mobilization and activities of enzymes in oxidative metabolic pathways. There is also general agreement that a reduction occurs of glycolytic activity, blood bicarbonate levels and body weight. However, the extent of these changes is neither consistent among species nor within similar experimental conditions.

Opinion is divided on the mechanism of several metabolic changes that occur in response to hypoxia. For example, body weight loss has been shown primarily as a loss of fat-free, lean body mass. Other studies have demonstrated that it is primarily a loss of adipose tissue. The investigators who support the latter hypothesis do not agree on the change in composition of blood lipids in hypoxia. Some investigators showed an increase in circulating saturated fatty acids, while others demonstrated a decrease in these acids. Another major subject of controversy is the metabolism of lactic and pyruvic acids during exposure to hypoxia. Some studies show a net increase of both acids in the blood, the change in lactate being greater than that of pyruvate. The results of other research indicate that blood lactate does not increase and the ratio of lactate to pyruvate widens due to a decline in blood pyruvate. Opinion is divided on the effects of hypoxia on nitrogen balance. The excretions of urea, ammonia and creatine increased in some studies and decreased in others.

Overall metabolism appears to be directed at fulfilling energy needs during exposure to hypoxia. Initially, fatty acids are mobilized from body stores and fatty acid oxidation replaces glycolysis as the primary energy pathway. Glycogenesis increases during this period and, as fatty acid reserves become sufficiently exhausted, glycogenolysis stimulates glycolysis. By the time reserves of glycogen are reduced, the body becomes acclimatized sufficiently to depend on the diet for energy. These changes are transitory during the initial weeks at high altitude. Because of the rapid changes and the diversity of the limited number of metabolic studies in conditions of high altitude, some of the data are contradictory and highly dependent on the extent and duration of hypoxia, times of sampling, the species studied and the dietary program. The above factors are all basic to the consideration of research at high altitude.

The National Institute of Agricultural and Livestock Research in Ecuador established that a high priority research need in the _sierra_ was an assessment of the potential of the _páramo_ for meat production. The present trial was designed to assess the feasibility of livestock production at an altitude above 11,600 feet. In a strict sense, the nutrient yield of the _páramo_ could have been determined by periodic sampling and analysis of the forages. However, estimates of livestock productivity based on laboratory data and actual animal productivity are often disparate. Therefore, both animal performance data and laboratory analyses were used to predict the utility of the _páramo_ for meat production on a practical basis. Land, animals and technical support were available for an extended period.

The following objectives were established:

1. To determine the nutrient yield of the _páramo_ throughout the year;
2. To determine the potential of the _páramo_ for the production of meat;
3. To determine those factors of nutrition and management of male bovines necessary to

establish a low-cost, profitable system of meat production which would provide additional meat for human consumption with a minimum shift of agricultural inputs away from existing production.

CHAPTER III

EXPERIMENTAL PROCEDURES

The experimental procedures of this trial were typical of those employed in research on cattle nutrition and management. The experiment required an extensive developmental effort because of its location. The extent to which the constraints were overcome determined the type of trial that was conducted.

Experimental Design

Forty-eight Holstein males selected from the dairy research herd of INIAP, at the Santa Catalina Experiment Station, were divided into two groups of twenty-four animals each. The forty-eight cattle averaged 254.6 kg body weight and 453 days of age. The animals were assigned to treatment groups according to body weight and age. Ten of the forty-eight head were bulls; the remainder were castrated at an early age.

One group of animals was assigned to graze at an altitude between 11,600 and 12,000 feet (3,550 and 3,650 meters), referred to as the "lower group." The other group was assigned to a pasture between 12,100 and 13,800 feet (3,700 and 4,200 meters) of altitude and was called the "upper group." The lower pasture was composed of approximately 170 acres (seventy hectares). The area of the upper pasture was about 295 acres (120 hectares). All animals were maintained at their respective altitudes for twelve and one-half months, from February 26, 1973, to March 13, 1974.

Experimental Site

The experiment was conducted in conditions of hypoxia and rugged terrain. The site was representative of the more remote *páramo* areas in the Western Range of the Andes in Ecuador.

Description

The physical characteristics of the experimental site were important determinants of the nature of the trial. An understanding of these features provides insight into the constraints of time and resources.

Location: The experimental site is on the eastern slope of the volcano Atacazo, which lies in the western ridge of the Andes, fifteen miles south of Quito, Ecuador, and twenty-three miles south of the Equator. The area is bounded by latitudes 0°20.2'S and 0°20.7'S and by the longitudes 78°35.2'W and

78°36.8'W. The site ranges in altitude from 11,600 feet to 13,800 feet (3,550 meters to 4,200 meters) above sea level. The lower portion of the site includes land of the Santa Catalina Experiment Station of INIAP and lies directly west of the station.

In Ecuador, the area above 11,800 feet (3,600 meters) of altitude up to the abrupt change from grass to the exposed rock face of mountain peaks is commonly called the páramo. The experiment was conducted entirely in the páramo and utilized the entire altitude range of this ecological area.

History: The experimental site had been used for occasional grazing and potato production until fifteen years ago. As is characteristic of the Ecuadorian highlands, centuries of experience have established that it is unprofitable to cultivate crops on the interior slopes of the western range of the Andes above an altitude of 11,500-11,800 feet. A clear division is readily visible throughout the sierra between the small, hand-cultivated plots just below this altitude range and the predominant light-green pastures that lie just above. There is often a buffer zone of approximately 100 to 300 feet containing small trees and bushes as the primary vegetation. The experimental site has all of these features and, to this extent, is representative of the high altitude zone of the country.

Management of the <u>páramo</u> throughout Ecuador is limited to burning which occurs in the dry season from June through September, the occasional grazing of sheep and cattle and the production of potatoes, cereal grains and pyrethrum.

<u>Topography</u>: The grazing area of the trial was generally in the shape of a narrow rectangle. It slopes upward from east to west with two large mesas at the lower and upper extremes, each of which likewise slope slightly upward from east to west. The lower mesa forms a large part of the pasture for the lower group and is located between 11,600 and 12,000 feet of altitude. The second mesa lies between 13,100 and 13,800 feet. The area between 12,300 and 13,100 feet altitude is a steep rise of 800 feet in a distance of 1,800 feet. The change in elevation from 12,000 and 12,300 feet occurs within a distance of 2,000 feet.

The lower half of the grazing area is bounded on the north by an erosion ditch from 15 to 30 feet deep. Three-fourths of the southern perimeter of the <u>páramo</u> is a cliff located above a narrow valley, the bottom of which is more than 600 feet below. This change in elevation occurs within a distance of less than 150 feet horizontally.

Climate: The climate of the *páramo* is cold, humid and windy. The average annual rainfall varies from 1,500 mm to 2,000 mm. The period of greatest precipitation is from October to March, when 70 percent of the annual rainfall occurs. Occasional sleeting occurs overnight, but thawing is rapid during the following morning. Measurable precipitation occurs on more than 200 days of each year. The average air temperature during the day is less than 10°C and is often below freezing during the night. The average monthly mean, minimum and maximum temperatures vary by only 2 to 3°C during the year. The area is covered with clouds more than 75 percent of the time with only small variation from one month to the next. The most cloud-free period daily is in the morning. The wind has an average speed of fifteen miles per hour and often gusts to between thirty and forty miles per hour. The humidity averages about 90 percent during the months of highest rainfall but declines to 40 to 60 percent in the period of least precipitation, June through September. The periods of high and low evaporation of soil moisture are opposite those of rainfall. The evaporation of soil water ranges from 35 to 115 mm per month, with an average of 60 mm monthly.

The barometric pressure ranges from 493 mm Hg at 11,600 feet to 444 mm Hg at 13,800 feet elevation.

The average length of daylight during the year is twelve hours, with a seasonal variation of one-half hour. Solar radiation averages 380.6 gram-Calories/cm^2/day.

Forages: The principal native forage is a highly fibrous, slow-growing grass, Stipa Ichu, commonly known in the United States as needlegrass and in Ecuador as paja de páramo. Paja is the Spanish word for straw. The páramo pasture consists of approximately 90 percent paja. It is the principal grass used in the highlands for roofs of grass huts of the rural Indian population. Another grass, Paspalum Virgatum, composes approximately 5 percent of the total forage in the páramo and is the second most predominant species there. It grows low to the ground, is wide-leafed and hirsute. Its appearance resembles the high quality grasses found at lower altitudes, but it has lower palatability than Stipa Ichu and is equal in fiber content. Between elevations of approximately 11,500 and 12,200 feet other species such as fescue, ryegrass and white clover are found. These forages will grow above this altitude if sown, but they are not native to the area. Lupines are scattered throughout the area, but these are not usually eaten by cattle. They are apparently of the bitter type and unpalatable during all stages of maturity. The lupines are found up to the higher limits of the páramo used for the experiment.

Stipa Ichu is low in palatability and nutritive value when mature but is an acceptable forage when young. After burning or grazing the regrowth is slow. When the soil is disturbed by plowing, harrowing or by concentrated animal activity, five or more years are required for the *paja* to again become established.

Soils: The deep, black soil of the site is of volcanic origin. The parent pumice layer lies from five to twenty feet below the surface. The average monthly soil temperatures at 50 cm depth vary from 7°C to 20°C, the average during the year is 10°C, and the average minimum temperature at the surface is -5.2°C. Because of low soil temperatures the decay of plant material is very slow, which has permitted the development of a deep topsoil layer high in organic matter. The soil is highly compacted, yet light rainfall is readily absorbed. When the soil is denuded of vegetation it erodes easily. Once disturbed by plowing or harrowing the soil is friable and easily worked for years afterward. The soil is very slippery when wet. Only an occasional stone is found in the topsoil, although there is often a layer of pumice of one to three inches in depth lying from one to five feet below the surface.

Development

The precursory and most difficult portion of the study was the development of the experimental area and access to the site. In contrast with typical animal nutrition research facilities in the United States, the site existed in its natural, centuries-old form, unexploited and with no prior preparation for research of this type. Access to the area was initially possible only on foot or with difficulty on horseback.

Land Acquisition: A major requirement of the study was to obtain a sufficient area of páramo pasture to support a large animal production study. The lower 170 acres was owned by INIAP. Potatoes had been grown there five years previously. This area could not be considered true páramo because Stipa Ichu was not the dominant species after a five-year fallow period. This area was suitable, however, for the construction of a corral and the animal weighing facility.

Because there was an insufficient area of true páramo under the control of INIAP, a site adjacent to the southern boundary of the station was inspected on a horseback ride of eight hours. This area was rejected because it would have been impossible to construct an access road above 10,800 feet of altitude. Another area, thirteen miles to the south on the volcano Curazón was inspected during a one-day horseback ride. Although there existed a road which could have been renovated up to 12,500 feet, this site was rejected because reconstruction of the road would have been too costly. In addition, the round trip from the experiment station to the site required two and one-half hours by vehicle and adequate supervision of the study would have been difficult. It should be noted that the owners of these two locations were highly interested in the study and offered full cooperation and unrestricted use of their land. It was because of this attitude, which is characteristic of the Ecuadorian people, that the area finally used for the trial was obtained.

A major necessity of the trial was for it to be located in close proximity to the experiment station for maximal management and control. The land adjoining the *páramo* of INIAP directly to the west was the property of two hacienda owners whose land extended from lower altitudes into the *páramo*. Unlimited and unrestricted use of the land was graciously offered for a year. This was especially difficult for one owner because he had already donated the major portion of the land needed for the study (from 12,500 to 13,800 feet of altitude) to a worker's cooperative. With the help of INIAP, a verbal commitment was made with the owners and the development of the site was begun.

Access Road: To best utilize the experimental area a road was constructed beginning at an elevation of 10,500 feet and finally reaching 12,100 feet in a distance of one and one-half miles, an average rise of 20 percent. The new road connected with the upper part of a road from the dairy cattle research center. The lower half of the new road was generally parallel to an erosion ditch fifteen feet deep. More than half of the road was cut into the side of a steep hill and required bulldozing as much as fifteen feet into the topsoil to provide a safe base for use by tractors and jeeps. One mile of the road had to be bulldozed through heavy timber and brush. This area could previously be traveled on foot and was only partially passable on horseback. Before the new road was built, a difficult ride of two hours on horseback was necessary to reach an altitude of 12,000 feet. An additional hour was required to reach 14,000 feet. After completion of the road, the central pasture area at 12,000 feet of altitude was reached by jeep in fifteen minutes.

Road construction began in April, 1973. Heavy rains prevented work on the road prior to that time and frequent rains from April to June made the road impassable by jeep or tractor. It was necessary to build a bridge across the erosion ditch which conducted a considerable quantity of surface drainage from the

higher altitudes of the mountain. Once the road had been cleared to the bridge site, heavy brush and small trees were pushed into the bottom of the erosion ditch and were covered with soil. This type of bridge construction (with the brush permitting passage of water) is common in rural areas. However, two weeks after completion an unusually heavy rain washed out the bridge.

A second bridge was constructed about 100 yards below the first location. Four cement tubes three feet in diameter and three feet in length were placed in the bottom of the erosion ditch and covered with soil. The bridge was narrow but passable and served well throughout the trial.

The road divided at an elevation of 11,800 feet with one section leading to the corral and the other to the pasture for the upper group. In the upper road a shallow bridge was constructed over the stream supplying water to the animals. A series of cement tubes was covered with soil. This bridge endured throughout the trial and required only minor maintenance.

The rainy season began again during the middle of the trial and lasted through the end. Periodic restoration of the road was necessary during this period because of erosion.

<u>Fencing</u>: The first section of fence installed was 2,000 feet in length and divided the two groups of steers at 12,100 feet of altitude. After several animals had either plummeted to their deaths over the cliff to the south or had fallen into the deep ditch to the north, additional fencing was constructed. The first addition to the divider fence was more than three miles long and was located so as to minimize the loss of animals. A group of twenty laborers worked on three consecutive Saturday mornings to dig postholes, set posts and string wire in the most critical locations. A group of five people worked each day for a month to complete construction. Every morning the workers were transported to the area by tractor and wagon, an ascent of one hour. To transport the workers and materials, approximately fifty round trips by tractor and wagon were required during construction of the fence.

The fence posts were long slabs of the trunk of mature bamboo-like trees. The slabs had a cross-section of approximately one inch by four inches and a height from eight to ten feet. The posts were set in holes three feet deep which were dug by hand at intervals of ten feet. Three strands of four-point barbed wire were attached to the posts with fence staples on the pasture side of the posts. The lower strand of barbed wire was located about eighteen inches from the ground, and there were about fifteen inches between each of the three strands. Gates made of barbed wire and small posts were constructed for the convenience of vehicle and animal movement.

Water Supply: One determinant for the selection of the experimental site was the availability of an adequate year-round supply of water at all altitudes. The principal water supply was a small stream running in a ditch averaging one foot in width and two feet in depth. The stream flooded in the rainy season and continued to flow in the dry season. The minimum water flow was approximately one gallon per minute.

The stream was supplied by the surface drainage of rainfall, and the melting of snow from the mountain, and flowed through the two pastures. It was easily accessible below 13,000 feet of altitude.

A portion of the upper mesa, between 13,000 and 13,400 feet of altitude, contained several stagnant or slow-flowing pools of clear water. These pools had the appearance of those described in Utah (24, 125), yet the water was clear and tasted fresh. The animals would readily consume this water, but the herdsman was instructed to prevent the cattle from using it.

To provide access for the cattle and assure a water supply at all times, over one mile of the stream was cleared of plants and brush and about one-fourth of this length was made wider and deeper. The stream was redirected for about 200 feet to serve better the animals in the upper group.

Corral: A corral measuring 90 x 180 feet and divided into two equal sections ninety feet square was constructed at 11,800 feet of altitude. A cattle chute was built along one long side of the corral and led to a portable balance designed for weighing livestock. The cattle entered the chute from one section of the corral and left the chute through the balance, entering the other section of the corral.

The perimeter of the corral and the center dividing fence were constructed with pine posts ten feet apart on which were stapled three strands of barbed wire. The heavy pine corner and gate posts were a minimum of eight inches in diameter and eight feet in length. The chute was constructed by using one long perimeter fence and building an interior fence parallel to and four feet from the perimeter fence. The pine posts used for the chute were six to eight inches in diameter, eight feet in length and placed six feet apart. Six strands of barbed wire were placed nine inches apart along the length of the chute. Bamboo slabs were placed parallel to the ground between the barbed wire strands to improve the strength of the chute and reduce injury from the barbed wire. Each section of the corral and the dividing fence had a gate for cattle access and a small walk-through gate for human use.

The portable scale was located at the exit of the chute. It was transported by tractor and remained on the site for ten months, until it was needed at the Pichilingue station of INIAP on the coast. Because a scale was required for subsequent weighings, INIAP purchased a new platform scale which was transported to the corral, placed in the same location as the previous one, and then calibrated.

Personnel: An essential feature of the study was the need to have a herdsman provide constant attention to the cattle. There were many days during which it was impossible to ascend to the *páramo* due to weather conditions, even on the access road. Early each day the herdsman fed mineral supplements, inventoried the cattle, checked for health problems and continually moved the animals around the pastures. After a short period of observations, it was obvious that they needed to be moved continually because without supervision they would graze for a short period and then lie down for much of the day. An additional benefit of a full-time herdsman on the experimental site was that his presence would minimize rustling.

There is a history of rustling from the high altitude area. Rustlers needed a cattle drive of only four to five hours to a road which could be used to transport the cattle from the area.

Initially, a man who lived above the station and was an employee of INIAP was assigned as herdsman. However, he became vital to other work at the experiment station and was subsequently unavailable. The man finally selected for the position was fifty-seven years old and had some experience with cattle at high altitude. He willingly assumed the duties as herdsman because it meant a 50 percent increase of salary. He applied his thumbprint to a contract for one year and made arrangements to move to the páramo. He was paid an equivalent of U.S. $1.52 per day for working seven days a week for the duration of the trial.

There is a union at INIAP which was in agreement with the terms of the contract. According to the contract the herdsman was responsible for "control of the animals day and night, including Saturdays and Sundays, as well as notifying appropriate personnel of sick animals, aiding in weighing the animals and maintenance of the water supply and fences." The herdsman performed many other duties as well, but required close supervision. A case in point was his reluctance to feed, as requested, mineral supplements daily in the early part of the trial.

The herdsman's move to the páramo was difficult for him, since he owned a house near the experiment station and had a family of five children from six months to fourteen years of age. Proper housing for the family was difficult to construct in the páramo. To have the family in the páramo would have required a considerable effort to maintain supplies of food there, especially with the road often being impassable. As a result, he spent much of his time alone and had only occasional visits with the family.

At the beginning of the trial the herdsman helped to move the steers from the station to the páramo. On the following day he began construction of a grass hut for his own use. The frame was constructed using the trunks of small trees. The walls and roof consisted of mature paja de páramo. The hut was located near water but not protected from the wind. Because the herdsman wanted more protection from the cold winds, a second large hut and a cooking shelter were constructed in a sheltered location using similar materials.

Management

After development of the site for the experiment, continual maintenance was required due to wear from the cattle, weather and trespassers.

<u>Access Road</u>: Frequent heavy rains were responsible for most of the maintenance required on the access road. The initial construction of the road resulted in a flat profile with a shallow drainage ditch on one side. This construction was unsatisfactory because water tended to collect in the middle and was not drained by the ditch. Approximately one mile of the road was then reconstructed with a crown so the road would slope away from the center on both sides. This change permitted faster drying of the surface and allowed the passage of vehicles sooner after a heavy rainfall.

A plan to construct a surface of stone on the road was deferred until late in the trial, due to a shortage of stone and of personnel experienced in this type of work. Approximately 300 feet of road was laid at the origin of the new road using stones broken by hand from large boulders. The road was about twelve feet wide. The stone surface provided excellent traction for vehicles and could be traveled even during heavy rains. The two men assigned to road construction completed from nine to twelve feet of road per day. This type of construction is appropriate for access to the <u>páramo</u> and is found on many small roads and some secondary roads in the <u>sierra</u>.

<u>Fencing</u>: Once the fence posts were firmly tamped into place, only periodic maintenance was required. The animals seldom passed through the fence, but younger animals in the upper group occasionally did so trying to reach the pasture of the lower group. This caused some of the maintenance required during the experiment.

A major maintenance problem was to replace the wire and posts that occasionally were stolen by Indians during the night. Gates were at times left open or poorly secured by mountain-climbing groups which frequently passed through the site.

<u>Water Supply</u>: Once the stream was cleared and enlarged, maintenance was limited to periodic clearing and rebuilding where cattle had broken away the sides which caused local flooding.

Another problem resulted in regular arbitration between the two land owners who controlled the source of water for the <u>páramo</u>. One owner periodically diverted the stream so as to increase the flow into a stream on his land. The other owner, whose land was being used in the experiment below 12,500 feet of altitude, responded by redirecting the stream through the <u>páramo</u> to provide water to his hacienda below. Periodic discussions with the owners resulted in their agreement to permit a constant water supply to the animals throughout the trial.

Corral: After the corral was constructed little maintenance was required. Occasional reinforcement of the cattle chute was necessary. The animal scale required leveling and calibration before each weighing.

Personnel: The herdsman was permitted to return to his home on Sundays, only for the time necessary to obtain food and supplies. His oldest son watched the herd on these occasions. The herdsman was responsible for directing the work of laborers in the páramo as well as providing mineral supplements to the cattle on a daily basis. The herdsman spent a portion of most days locating animals that were missing after his daily inventory. Steers would wander to other páramo areas and up to three hours were spent in bringing them back. Other missing animals were found to have fallen into ravines or over the cliff. Those in ravines occasionally were injured or had died, and several hours of digging were required to make a slanted path to extricate each animal.

Experimental Animals

The younger animals were reserved for this study several months ahead of its initiation. All of the steers were maintained in a pasture located just below the lower limit of the páramo, varying in altitude from 10,500 to 11,000 feet. The animals were brought down to the research center in January, 1973, for selection, weighing and identification.

Genetic History

The foundation stock of the herd was derived from two sources. The original stock was purchased in the mid-1960s from Holstein breeders in Ecuador and consisted of cattle variously upgraded from Holstein-*mestizo* crosses. The *mestizo* is the native stock, originating from shipments made by Spain and other European countries after the conquest. The other source of the foundation stock was a donation from the Dutch government as part of a six-year cooperative research and training program that began in 1966. The donation consisted of twenty-four purebred Holstein-Friesians, consisting of twenty heifers and four bulls. Subsequent breeding between the two groups produced many male calves, forty-eight of which were made available for the *páramo* trial.

Feeding Regime

All animals were allowed *ad libitum* consumption of forage, water and minerals. No concentrate feeds were offered during the trial.

Pasture: The primary feed source for the steers was the native *páramo* pasture, composed of more than 90 percent *Stipa* (*paja*) and some *Paspalum*. The animals grazed during most of the daylight hours and periodically during the night. The *paja* was abrasive and caused the hair on the muzzle of the animals to wear off after they grazed for a period of three weeks.

Mineral Supplements: Throughout the trial, mineral supplements were provided for *ad libitum* consumption. The animals received two types of supplements. The first type, "Ecuasal," was offered sporadically during the first eight months of the trial. The composition is shown in Table 6. This mixture of macroelements and microelements was formulated by the Dutch technicians in the late 1960s and was placed into commercial production for general use in the *sierra*.

Table 6

Mineral Composition of Trace Element Mixture (Ecuasal)

Ingredient	Percentage of Total Mixture
NaCl	96.8
Manganese	0.20
Iron	0.16
Copper	0.033
Cobalt	0.010
Iodine	0.007
Zinc	0.005

The trace element mixture was readily available and was fed to the dairy herd at the experiment station.

The complete mineral supplement for the dairy herd consisted of a mixture of equal parts Ecuasal and steamed bone meal.

One of the first steps in the plan of the trial included the sampling of blood, forages and soil to determine the mineral status of the *páramo*. Ecuasal was used as an interim supplement. Once the analyses were completed, a mineral mixture appropriate for the *páramo* was formulated for use in the trial. However, several months were required to analyze the samples. This was because the Nutrition Laboratory was unable to analyze confidently for microelements due to a variety of constraints, the principal one being long delays of essential supplies in the customs office.

After eight months of the trial the analyses were completed and the appropriate mineral mixture was formulated and offered to the animals. The composition of this mixture is shown in Table 7. The mixture was balanced to meet the most serious mineral deficiencies in the animals (199, 254, 255). It should be noted, however, that the mineral requirements were calculated using standards established in low-altitude conditions. It is possible that the requirements for and the tissue levels of these elements may differ at high altitude.

Table 7

Composition of the Mineral Supplement Used in the *Páramo*

Ingredient	Percentage of the Ingredient	Percentage of the Total Mixture
Bone meal	----	30.8
Calcium	30.5	9.4
Phosphorus	14.3	4.4
Gypsum	----	18.0
Calcium	23.3	4.2
Sulfur	18.6	3.3
Sulfate	55.8	10.0
Muriate of potash	----	12.8
Potassium	52.4	6.7
Urea	----	12.8
Nitrogen	45.0	
Molasses	----	25.6

The balanced mineral supplement was mixed at the experiment station and transported weekly to the *páramo*. The ingredients were purchased especially for the trial.

In the *páramo* the first supplement was placed in half-sections of tractor tires and maintained in a quantity sufficient for *ad libitum* consumption. Frequent heavy rains and strong winds made it necessary to place only small amounts of the mixture in the tires because much was lost.

The second mineral supplement was offered daily in amounts measured to equal consumption and yet maintain *ad libitum* intake. Special wooden feed bunks were constructed at the experiment station and placed in the upper and lower pastures. The size of the feed bunks permitted all animals in each group to feed from them at the same time.

Water Supply: To assure that the animals received an adequate amount of water, they were moved to the stream once each day. At other times they were allowed free access to the water as they needed it.

Grazing Management

The herdsman preferred to work on foot rather than use a horse because he received a serious injury on horseback a year before the trial began. His mobility was reduced but not enough to affect his daily routine. Because the study focused on the use of native forage, no renovation of the pastures by seeding or tillage occurred.

Movement of Animals: The herdsman offered the cattle their daily allotment of minerals at daybreak, took inventory and then rounded up missing animals. He spent the remaining daylight hours alternating between the upper and lower groups, moving them into areas of the pasture that had not recently been grazed and preferably into sections containing *paja* in the early stages of growth. At dusk the herdsman brought the cattle in the upper group down to the lower portion of their pasture. This area was nearer to his residence and provided some protection from the wind.

Pasture Burning: A common practice in the páramo throughout Ecuador is the periodic burning of paja when it is mature. This occurs during several months of the dry season when rains are less frequent and the plants have matured to such a height that the fire will be able to spread. Mature paja has a high dry matter content and is readily ignited. The strong winds cause the fire to spread rapidly with little heating of the soil. Because the plants grow in bunches one to two feet apart, the fire cannot spread continuously through areas of low plant density or early maturity. Due to irregular terrain, ditches and bare spots, the largest of fires can cover only a few acres without frequent relighting.

The land in the páramo is undulating and broken with many small erosion ditches, which makes it difficult to use machinery for pasture maintenance and renovation. It is for these reasons and because of the difficulty, often the impossibility, of access to páramo areas, that burning is an accepted method of renewing the growth of grass on a seasonal basis. Many of the fires, however, are set by the Indians without any special purpose.

Health Measures

The diagnosis of health problems was facilitated by the assistance of two veterinarians on the staff of the Dairy Research Center of INIAP. These men received their degrees in Ecuador and had gained experience with INIAP. They assisted in training the herdsman and were eager to participate in the conduct of the trial.

Brisket Disease: Because of many cases of brisket disease reported at the experiment station (10,000 feet above sea level) the animals in the *páramo* were checked continually for symptoms. These symptoms included the accumulation of edema in the brisket area, under the jaw and in the abdominal tissues; excessive pulsing in the jugular vein; and lack of appetite.

Pneumonia: The climate of the *páramo* is conducive to the development of pneumonia and other bronchial disorders. Diagnosis and treatment of the disease was performed by the veterinarians of INIAP.

Parasites: Livestock are always susceptible to infestations by internal and external parasites. Daily observations of the cattle were made to determine early any diarrhea. All animals were examined periodically for the presence of lice. Ticks are not found at high altitude, although they abound below 8,000 feet.

Brucellosis and Tuberculosis: The incidence of brucellosis and tuberculosis in Ecuador is very high. All animals were subjected to the routine testing and control programs of INIAP.

Hoof and Mouth Disease (Aphthous Fever): All animals were vaccinated before being sent to the páramo and every three months during the trial.

Hemorrhagic Septicemia: The veterinarians vaccinated all animals at six months of age as part of the health program of INIAP.

Post-mortem Examination: Autopsies were performed by the veterinarians both in the páramo and at the Dairy Research Center. The examinations included microbiological culture, microscopic screening and inspection for gross lesions of all organs and tissues.

Sample Collection

Due to a variety of factors, principally the weather, an unfinished road surface and the unavailability of essential supplies, the sampling periods were irregular. Almost daily during the wet season, the rainfall began early in the afternoon, continued through the night and ceased early the following morning. Travel to the site was usually impossible unless the road had dried for several hours. Four to six hours were required to complete weighing and sampling each day, of which travel time for a round trip was about one-half hour, at least one and one-half hours were required to weigh the animals, and the blood sampling occupied three to four hours.

Body Weights

All of the cattle were weighed on scales designed for large animals. Body weights were measured in kilograms for the first and last two series of weighings and in pounds on the remaining dates. This was because different scales were used during the trial. All weights in pounds were converted to kilograms by using a multiplier of 0.454. Each animal was weighed after he became settled in the scale and was making no noticeable movement. Animals were often reweighed to check previous weights and scale performance. The scales were calibrated using known volumes of water and bags of cement weighed on scales officially checked by the government of Ecuador. Large quantities of known volumes of water were difficult to transport to the páramo. Smaller volumes of water, up to twenty kilograms, were weighed on the scale alone, and with small and large animals on the balance. The water also served to check the bags of cement used for calibration. The net weight was consistent across the range of weights to which the scales were subjected.

Blood

Blood samples were taken from all steers surviving at 139, 280 and 384 days of the experiment. Control samples were taken from cattle at the dairy cattle research center.

Jugular venipuncture was used to obtain all blood samples. Each sample collection consisted of two venipunctures in the right jugular vein of each animal less than two minutes apart. The first was made using a plastic shield fitted with a disposable 20-guage needle (Vacutainer[R], Becton-Dickinson, Rutherford, N.J.). Immediately after venipuncture the small stream of blood flowing from the needle was directed into a disposable heparinized hematocrit tube graduated into 105 divisions and measuring 10 cm in length and 2 mm inside diameter. After filling the hematocrit tube a 16x127 mm Vacutainer[R] tube was forced onto the needle and filled to a height of 9 cm, resulting in a volume of approximately 10 ml. This tube contained the anticoagulant potassium oxalate (30 mg) and sodium fluoride (37 mg). The latter was used to stop glycolysis in the sample. The needle was withdrawn from the vein, the tube removed from the shield and tipped end-to-end to allow gentle mixing of the blood with the potassium oxalate and sodium fluoride.

The second jugular venipuncture was made using a 14-guage needle to obtain a large quantity of blood serum. A volume of at least 250 cc was collected in a glass or polyethylene container having a tightly sealing top. The container was previously rinsed in triple-distilled water and dried. The blood was taken to the experiment station and prepared for storage and analysis.

Ages of Animals

The ages of the animals were determined from herd registry records maintained at the Dairy Cattle Research Center at the Santa Catalina Experiment Station. For convenience in calculations the age in years and months was converted to days.

Identification

All animals were the offspring of the dairy herd at the Santa Catalina Experiment Station. The standard practice of identification included making a drawing of the calf shortly after birth and placement of a herd ear tag in the left ear and recording the number.

During preparation of the animals for the trial, those which had lost the original ear tags were retagged and the numbers recorded. Each animal in the trial was checked against its registered drawing and ear tag number for positive identification.

Once positive identification was made, all animals were freeze-branded using a mixture of dry ice and ethyl alcohol. The temperature of this mixture is -72°C. The branding irons were in the shape of numerals. The branding iron was placed in the mixture for at least two minutes, then pressed for thirty seconds against the skin of the animal in an area covered with black hair. The numbers used ranged from one to forty-eight. Freeze-branding was used to facilitate identification of the animals during observation without having to catch and restrain them. This was particularly convenient for the herdsman during his daily inventory, health check and separation of those animals that occasionally changed groups overnight. Because all of the animals were corralled and randomly weighed at the same time, the freeze-brands permitted easy identification without further restraint.

Forages

Samples of young and mature *Stipa* and *Paspalum* were collected by cutting representative plants by hand at a height above the crown similar to that of plants remaining after the animals had grazed the area. This height was 5-10 cm for young plants of both species, 20-40 cm in mature *Stipa* and 10-20 cm in mature *Paspalum*. Each sample collected for analysis was composed of ten cuttings taken on a zig-zag course from east to west, transversing the main grazing area, a change in altitude of 11,600 feet to 13,200 feet. Composite samples of forage weighing at least 500 grams were placed in plastic bags and sealed for subsequent processing and analysis in the Nutrition Laboratory.

Soil

Samples of soil were taken along a line similar to that used for forages. The samples were composed of twenty-five plugs of soil taken to a depth of 20 cm with a soil borer measuring approximately 2.5 cm inside diameter. The samples were analyzed by the Soils Laboratory of the Santa Catalina Experiment Station.

Meteorological Data

Due to a lack of equipment and disinterest on the part of the National Meteorological Service of Ecuador, that organization provided no direct assistance in the collection of weather data for the *páramo* area during the trial. One of the three Class I weather stations in the *sierra* is located at the Santa Catalina Experiment Station, at an altitude of 10,000 feet and directly east of the experimental site. This station records complete meteorological data for the area and provided an estimate of rainfall, temperature, winds and humidity for the *páramo*.

Altitude

The various altitudes referred to in the study were measured directly with an altimeter accurate to the nearest forty meters. These determinations were checked by using the high quality topographic maps, with forty-meter contour intervals, published by the Military Geographical Institute of Ecuador. This institute has excellent equipment, is staffed with highly trained personnel and produces a variety of maps for the country. The topographical maps were also checked by use of aerial photographs of the area.

Area of the Site

The area of the site was determined by using high-precision aerial photographs and topographical maps. To determine the precision of these aids, reference points on the photographs and maps were measured on the ground with a 100-meter steel measuring tape.

Analytical Methods

The analyses of blood and forage were made in the Nutrition Laboratory of INIAP, at the Santa Catalina Experiment Station. Soil samples were analyzed in the Soils Laboratory in the same facility. The Nutrition Laboratory resulted from a cooperative research and training program between INIAP and the Government of Switzerland. INIAP provided land and buildings for the

facility while the Swiss government donated laboratory equipment and supplies, as well as highly trained personnel to develop the analytical methods and train Ecuadorians in these procedures. After two years of diligent preparation, the laboratory was well-equipped with analytical instruments and supplies.

Macroelements and Microelements in Blood

The blood collected by jugular venipuncture was transported to the laboratory within five hours. All samples were maintained at a temperature of 7-10°C until processed in the laboratory.

Preparation and Storage: Upon arrival in the laboratory, the one-liter containers of blood were placed at a temperature of 4°C for 18-20 hours to permit thorough coagulation to obtain a maximum amount of serum. The serum was decanted into either polyethylene or glass bottles that were previously washed, rinsed with double-distilled water. The serum was stored at 4°C until analysis.

Atomic Absorption Spectrophotometry: All analyses of macroelements and microelements were performed by atomic absorption spectrophotometry. The instrument used for most of the samples was a Perkin-Elmer Model 103 atomic absorption spectrophotometer

(Perkin-Elmer Corp., Norwalk, Conn.). The analyses of blood samples from the final sampling period and the microelements not detected by the Perkin-Elmer 103 were performed on a Perkin-Elmer 303 double-beam atomic absorption spectrophotometer. This instrument, which has a greater sensitivity than the Model 103 spectrophotometer, was placed in service less than one month prior to the author's departure from Ecuador. All analytical procedures for blood minerals were developed by Perkin-Elmer, Inc. and adapted for use at INIAP by laboratory personnel (184).

Calcium: The container of serum was allowed to reach room temperature, then rotated gently to mix thoroughly the contents. A volume of 0.2 ml serum was added to a tube containing 5.0 ml of a solution of 0.1 percent lanthanum. The contents of the tube were gently mixed then aspirated into the spectrophotometer. A study comparing direct dilution of the serum versus trichloroacetic deproteinization demonstrated a higher recovery of calcium using direct dilution.

Calcium standards were prepared using 99.8 percent pure $CaCO_3$ that was dried two hours at 85°C before weighing. A weight of 1.2512 gm $CaCO_3$ was placed in a one-liter ground-glass stoppered volumetric flask. Volumes of 200 ml double-distilled water and 10 ml concentrated HCl were added, the contents mixed, then diluted to one liter. This solution was the stock standard and contained 500 ppm calcium. A working standard solution of 100 ppm Ca was prepared by placing 100 ml of stock standard in a 500 ml volumetric flask and diluted to 500 ml with double-distilled water containing 0.1 percent lanthanum. The standard curve was prepared by making dilutions from the working standard resulting in the following concentrations of calcium: 0.5, 1.0, 2.0, 3.0, 5.0 and 10.0 μg/ml.

The lanthanum solution was prepared by placing 58.64 gm La_2O_3 in a one-liter volumetric flask. Fifty milliliters of double-distilled water were added to the flask, mixed with the La_2O_3 followed by the addition of 250 ml of concentrated HCl. The contents were thoroughly mixed, then made up to one liter with double-distilled water. The stock standard solution contained 50 mg La/ml. The working standard solution was made by pipetting 20 ml of stock standard into a one-liter volumetric flask and diluting to volume with double-distilled water, making a concentration of 1 mg La/ml.

The standards and unknowns were read directly on the spectrophotometer as percentage absorption. The conversion of percentage absorption to concentration was calculated by computer.

Magnesium: The serum and standards were prepared using a procedure similar to that employed in calcium determinations. A stock standard of 1,000 ppm Mg was prepared by placing 1.0000 gm of magnesium shavings in a one-liter volumetric flask, dissolving the contents with 5.0 ml of HCl, and then diluting with double-distilled water up to one liter. The working standard was prepared by diluting 10 ml of stock standard to volume in a one-liter volumetric flask with a solution of 0.1 percent lanthanum, making a final volume of 10 μg Mg/ml. Appropriate dilutions were made to produce a range of standards for the standard curve having concentrations of magnesium of 0.5, 0.7, 1.0, and 1.5 μg/ml.

Sodium: The serum for sodium analysis was prepared by diluting the final solution which was used for potassium determinations. This dilution was made by pipetting 1.0 ml of the potassium dilution into a test tube, followed by the addition of 10.0 ml LiCl solution. This diluted mixture was aspirated directly into the spectrophotometer.

The stock standard for sodium analysis contained 1,000 ppm sodium. It was prepared by adding 2.3163 gm of sodium carbonate (99.5 percent purity) to a volumetric flask and diluting to one liter with a solution of lithium chloride (2 mg LiCl/ml).

The concentration of the working standard was 20 μg Na/ml. It was prepared by pipetting 20.0 ml of the stock standard into a volumetric flask and diluting to one liter with the lithium chloride solution.

The standard curve was established by making appropriate dilutions with lithium chloride solution to achieve concentrations of 0.05, 0.1, 0.2, 0.3, 0.5, 1.0 and 2.0 μg Na/ml.

Potassium: A volume of 0.2 ml serum was diluted with 5.0 ml of a 2 mg/ml solution of lithium chloride in a test tube and agitated on a test tube mixer. Test tubes were used for serial dilution because there were insufficient quantities of volumetric flasks available for the analyses. A second dilution was made by pipetting 1.0 ml of the first dilution into another test tube. This was followed by the addition of 10.0 ml of a solution containing 2 mg LiCl/ml, resulting in a final dilution of the serum of 1/286. This solution was aspirated directly into the spectrophotometer.

The lithium chloride solution (2 mg LiCl/ml) was prepared by adding 2.0000 gm anhydrous LiCl to a volumetric flask and diluting to one liter with double-distilled water. The solution was stored in polyethylene bottles.

The potassium stock standard was prepared by placing 1.9089 gm of 99.9 percent purity potassium chloride in a 1,000 ml volumetric flask and diluting to one liter with the lithium chloride solution. The final concentration was 1,000 ppm of potassium. This solution was stored in a polyethylene bottle. The working standard had a concentration of 100 ppm potassium and was prepared by making appropriate dilutions from the stock standard using the lithium chloride solution.

The standard curve was determined using the concentrations of potassium of 0.1, 0.2, 0.3, 0.5, 1.0, and 2.0 μg K/ml.

Serum Iron: Total serum iron was determined using 20 percent trichloroacetic acid digestion. A volume of 5.0 ml serum was added to a test tube containing 5.0 ml 20 percent TCA. The contents were mixed vigorously on a test tube mixer then maintained at 90°C for fifteen minutes. The digest was allowed to cool, then centrifuged at 2,500xg for fifteen minutes. The supernatant was aspirated directly into the spectrophotometer.

The stock standard was prepared by placing 4.9848 gm $FeSO_4 \cdot 7H_2O$ (99.9 percent pure) in a one-liter volumetric flask and diluting to one liter with double-distilled water, making a concentration of 1,000 ppm Fe.

A working standard of 10 ppm Fe was prepared using 10.0 ml of stock standard diluted to one liter in a volumetric flask. Appropriate dilutions were made to produce a standard curve using Fe concentrations of 0.5, 1.0, 3.0, 5.0 and 10.0 μg Fe/ml.

Hemoglobin-bound Iron: A 26-fold dilution of whole blood was made by pipetting 0.2 ml whole blood into a test tube followed by the addition of 5.0 ml double-distilled water. The contents of the tube were thoroughly mixed and aspirated directly into the spectrophotometer.

The stock standard and working standard solutions were the same as described above for serum iron. The concentrations used to develop the standard curve were also identical to those used for serum iron.

Hematocrit

The heparinized hematocrit tubes were filled by jugular venipuncture, transported to the laboratory and centrifuged at 2,500xg for fifteen minutes. Each tube was graduated into 105 divisions. The hematocrit, or packed cell volume, and the total volume were read directly to the nearest division and recorded. The percentage of packed cell volume was calculated and expressed as the hematocrit.

Forage Macroelements and Microelements

All macroelements and microelements in forage were determined by the Nutrition Laboratory using standard analytical procedures developed by the Perkin-Elmer Corporation (184). The results of the laboratory analyses were calculated on a dry matter basis and an as-fed basis.

Proximate Analysis of Forage

The Nutrition Laboratory performed the proximate analysis of all forage samples. The analysis was made according to its standard procedures which are similar to those used in the United States. Each analysis included the contents of dry matter, crude protein, crude fiber, ash and fat. Nitrogen-free extract was determined by difference.

The percentage dry matter was determined by weighing approximately 100 grams of forage before and after drying the sample in an oven for twenty-four hours at 105°C.

The crude protein content of forage was determined by Kjeldahl extraction of total nitrogen by sulfuric acid and sodium hydroxide digestion. The total nitrogen content was multiplied by 6.25 to provide an estimate of the concentration of protein.

Forage crude fiber was determined by digesting the dry matter with 0.7 percent sulfuric acid followed by a rinse with boiling double-distilled water. The residue was dried overnight at 105°C and then weighed.

The fat content of forage was determined by a seven-hour extraction with petroleum ether. The specifications of the product indicated the boiling point range was 40-60°C. However, under the altitude conditions of the laboratory, this range was 25-45°C. The calculation of the contribution of fat to total digestible nutrients was made by multiplying the fat content by 2.25.

Total ash or minerals in the forage was determined by weighing 10.0000 grams of forage dry matter before and after ashing in a muffle oven for 15 hours at 600°C. The residue was extracted for mineral analysis using hydrochloric, perchloric and nitric acids, followed by appropriate dilutions.

In Vitro Digestibility of Forage

In vitro dry matter and organic matter digestibility determinations of forage were made by a modified (4) Tilley and Terry method (251). The rumen inoculum was obtained from a fistulated steer grazing on pastures of ryegrass and clover. The method employed forty-eight hours of *in vitro* digestion, followed by forty-six hours of pepsin digestion. Organic matter determinations included ashing in a muffle furnace for three hours at 500°C. The silica content was multiplied by a factor of 3.0 and subtracted from the estimates of digestibility (4).

Cell-wall Constituents of Forage

Neutral-detergent fiber, acid-detergent fiber, acid-detergent lignin, silica and ash were determined by Oleas (203) according to the analytical procedures developed by the Agricultural Research Service (4). Neutral-detergent analysis provided an estimate of total fiber. Acid-detergent fiber analysis estimated the lignocellulose content. Acid-detergent lignin determinations estimated the lignin content. Because most of the insoluble ash content of forages consists of silica, the determination of ash provides an estimate of silica content.

Soil Macroelements and Microelements

Soil elements were analyzed by the Department of Soils at the Santa Catalina Experiment Station. The analyses were made by atomic absorption spectrophotometry according to procedures developed in the United States and adapted to conditions of the Laboratory.

Statistical Analysis

Analysis of variance was calculated for all animal measurements. Comparisons were made between the lower and upper groups for mean body weights, age, hematocrit and serum mineral concentrations. These comparisons were made for the three analytical categories which were:

1. All steers surviving on each measurement date (all steers);
2. Steers that survived the entire experiment (final group); and
3. Steers that died before the end of the trial (intermediate group).

Correlations were calculated for mean body weight and age, age and hematocrit, and serum iron and hemoglobin-bound iron. Multiple regression analysis was performed on the changes in mean body weight with time for the final group of steers. This analysis included both the separate and combined mean body weights of the lower and upper groups, before and after mineral supplementation and for the entire experiment.

CHAPTER IV

RESULTS AND DISCUSSION

This chapter is divided into two principal sections: (1) data that were obtained from the measures of animal performance, disease and blood samples; and (2) analyses that were relevant to the experimental site, including those of forages and soils.

Experimental Animals

A notable aspect of the study was the high mortality and abnormal behavior of the animals during their exposure to high altitude. Both the upper group and the lower group were composed of twenty-four animals at the beginning of the trial. At the last time of measuring, the number of steers was reduced to seventeen in the lower group and twelve in the upper group.

The principal data are derived from the twenty-nine steers remaining at the conclusion of the experiment. These animals are referred to in the tables and figures as the "final" group. Because these steers survived the entire experiment, changes of body weight and blood constituents in this group provide the best estimate of metabolic response throughout the trial.

A second set of data presented in tabular and graphic form was derived from the measurements of all animals surviving at each time of measurement. This category is denoted in the tables and text as the "total" group, or as "all steers" remaining at a specific stage of the experiment.

The third type of data consists of only the measurements of steers that did not survive to the end of the experiment. This group is referred to as the "intermediate" group in the tables and text.

An examination of the three types of data not only provides an insight into the responses of the steers to the experimental conditions, but also assists the separation of true responses from survivors and non-survivors. The most relevant data derive from those steers that survived the experiment, which was determined by <u>ex post facto</u> selection based on mortality. Although measurements of means are relevant at each time of sampling for all data, the changes in these means from one measurement to the next can be best understood in the group of surviving steers.

The numbers of animals in each analytical category ("all steers," "final" and "intermediate") surviving at each measurement or sampling date is presented in

Table 8. The terms "lower group" and "upper group" refer to the steers at the two respective treatment altitudes.

Body Weight Measurements

All animals were weighed six times in a period of 384 days (Table 9). Each consecutive interval is referred to as period I, II, III, IV, or V. The dates and number of days in each period are presented in Table 10. All animals were weighed each day for three consecutive days in February and July, 1973 and March, 1974. In October, 1973 all animals were weighed three times in a four-day period. The body weights in November, 1973 and January, 1974 were obtained from measurements taken on one day in each of those months. The number of days in period I extended from the middle date of the three weighings in February, 1973, through the middle date of the weighings in July, 1973. The periods II-V began on the day following the middle date of the previous weighings or single weighing, and included the middle date or single date of the subsequent weighing. There was a total of 386 days from the first to final weighings. Each experimental period was calculated using the mean dates of each series of weighings (Table 10). The total number of days in the trial was calculated as the sum of the periods. The mean dates correspond with the mean body weights.

Table 8

The Number of Animals Included in Analytical Categories on Each Day of Blood-Sampling or Weighing

Day	Lower Group			Upper Group			Lower and Upper Group		
	All Steers	Final	Inter-mediate	All Steers	Final	Inter-mediate	All Steers	Final	Inter-mediate
	----------------------------Number of Animals----------------------------								
0	24	17	7	24	12	12	48	29	19
139	21	17	4	20	12	8	41	29	12
238	19	17	2	16	12	4	35	29	6
280	19	17	2	15	12	3	34	29	5
330	19	17	2	12	12	0	31	29	2
384	17	17	0	12	12	0	29	29	0

Table 9

The Dates and Days of the Experiment at Each Weighing of All Steers

Dates of Weighings	Mean Date of Each Weighing	Day of the Experiment
Feb. 20, 21, 22, 1973	Feb. 21, 1973	0
Jul. 9, 10, 11, 1973	Jul. 10, 1973	139
Oct. 15, 17, 18, 1973	Oct. 17, 1973	238
Nov. 28, 1973	Nov. 28, 1973	280
Jan. 17, 1974	Jan. 17, 1974	330
Mar. 11, 12, 13, 1974	Mar. 12, 1974	384

Table 10

The Dates and Number of Days in Each Weighing Period

Number of Period	Median Dates of Each Period	Number of Days in Period
I	2/21/73 - 7/10/73	139
II	7/11/73 - 10/17/73	99
III	10/18/73 - 11/28/73	42
IV	11/29/73 - 1/17/74	50
V	1/18/74 - 3/12/74	54
I-V	2/21/73 - 3/12/74	384

The intervals between weighings were irregular due to highly variable and extreme weather conditions throughout the experiment. During the months of February through June, 1973, the rains were abnormally heavy and prolonged and prevented the transport of the scale to the site. In addition, essential sampling equipment and reagents were not available until June, 1973. The short intervals in periods III, IV and V resulted from the need to check more frequently the body weight changes of the animals after they were given a balanced mineral mixture.

Mean Body Weights: The mean body weights for the final group of steers, which consists of those animals that survived the experiment, are shown in Table 11. The initial body weights of the final group were higher for the lower and upper groups than those for all steers (Table 12). The initial mean body weight of the upper group was greater than the lower group. Continuous increases of mean body weight during the trial were noted for both groups. The mean body weights during the last two weighings for the lower group and for the last weighing for the upper group were significantly different from the respective initial mean body weights. The data of Table 11 are presented graphically in Figure 2. Over 50 percent of the total body weight

Table 11

Mean Body Weights of the Final Group of Steers on Each Weighing Date

Day of the Experiment	Lower Group N = 17	Upper Group N = 12
	Kilograms[a]	
0	294.3 ± 81.8[b, c]	304.2 ± 78.5[d]
139	295.5 ± 77.8	310.5 ± 72.8
238	320.0 ± 86.6	318.8 ± 81.9
280	321.8 ± 93.1	319.6 ± 88.0
330	334.4 ± 97.2[b]	338.5 ± 90.6
384	339.9 ± 96.7[c]	347.4 ± 84.5[d]

[a]All data are mean body weights ± standard deviation.

[b]Means sharing the same superscript are significantly different ($P < .10$)

[c, d]Means sharing the same superscript are significantly different ($P < .05$)

N = Number of animals

Table 12

Mean Body Weights of All Steers on Each Weighing Date

Day of the Experiment	N	Lower Group Mean BW	N	Upper Group Mean BW
		----------------Kilograms[a]		-----------------
0	24	254.6 ± 94.5[b,c,d,e]	24	254.6 ± 97.2[f,g,h]
139	21	264.7 ± 95.0	20	264.8 ± 96.5
238	19	302.0 ± 97.5[b]	16	292.4 ± 103.8
280	19	303.4 ± 103.6[c]	15	304.1 ± 102.9[f]
330	19	314.6 ± 109.2[d]	12	338.5 ± 90.6[g]
384	17	339.9 ± 96.7[e]	12	347.4 ± 84.5[h]

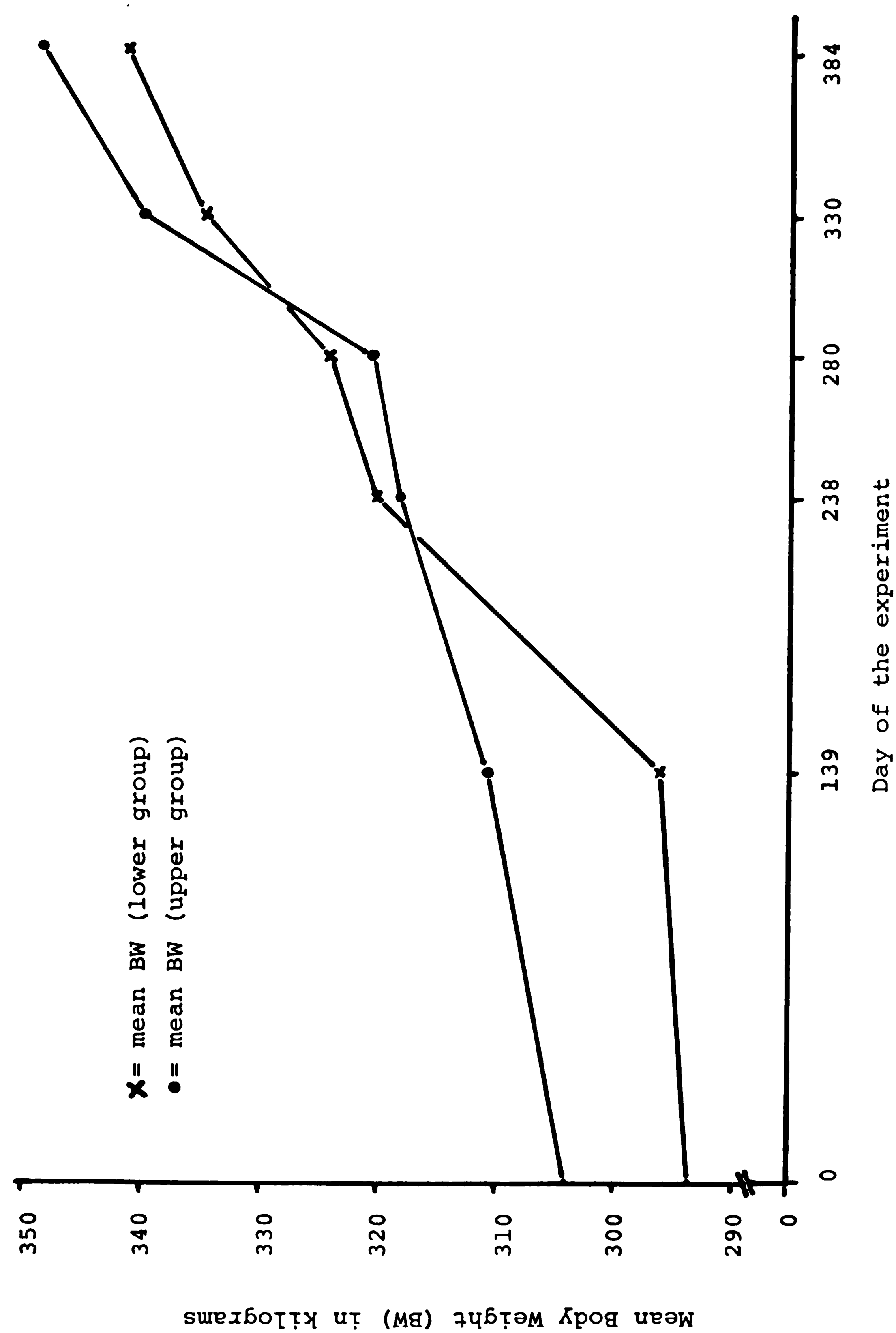
[a]All values are mean body weights ± standard deviation

[b,c,f]Means sharing the same superscript are significantly different ($P < .10$)

[d,e,g,h]Means sharing the same superscript are significantly different ($P < .05$)

N = Number of animals

Fig. 2. Mean Body Weights of the Final Group of Steers on Each Weighing Date



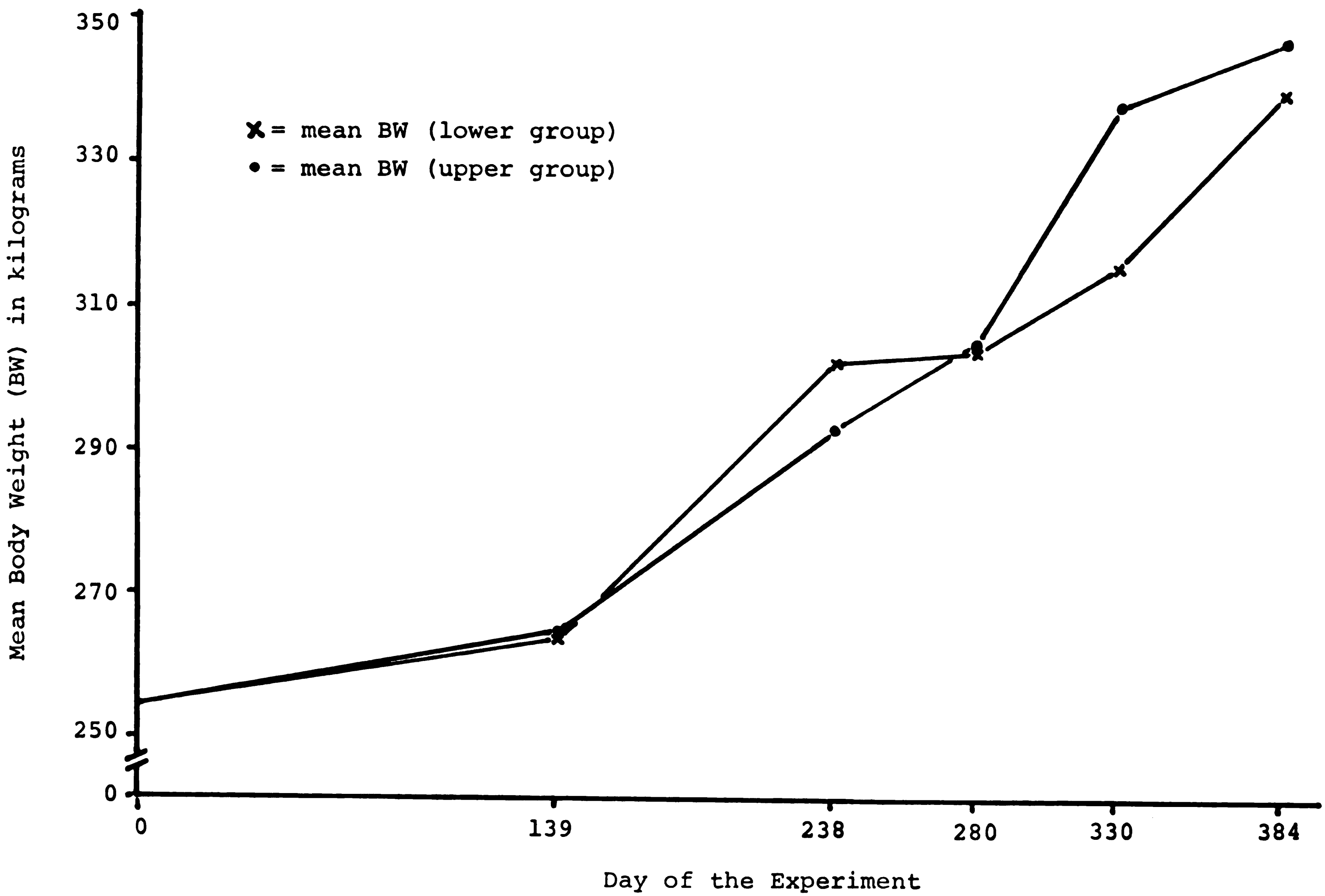
Mean Body Weight (BW) in kilograms
350
340
330
320
310
300
290
0
Day of the experiment
0
139
238
280
330
384
= mean BW (lower group)
= mean BW (upper group)

gain in each group occurred during the last 104 days of the 384 days of the trial. This period corresponds to the supplementation of the diet with a balanced mineral mixture.

The mean body weights of all steers surviving at each weighing are presented in Table 12. At the beginning of the trial both the lower and upper groups were selected to provide equal mean body weights for each group. There was a positive change of mean body weights for both groups from each weighing to the next (Table 12). These data are also illustrated in Figure 3. It can be seen that there was a slight gain in the body weight of both groups during the first 139 days which was the period of greatest acclimatization. Adaptation to the conditions of the experimental site probably continued beyond this time. The last mean body weights of the steers in both groups were significantly greater than the initial body weights. The mean body weight of the lower group at 330 days was significantly greater than its initial body weight.

The mean body weights of those animals surviving at each weighing, but not surviving to the end of the trial, the "intermediate" group, are shown in Table 13. An inspection of these data and those of Table 12 suggest that those animals having a lower mean body weight did not survive as well as those having higher initial

Fig. 3. Mean Body Weights of All Steers on Each Weighing Date



350
330
310
290
270
250
0
Mean Body Weight (BW) in kilograms
X = mean BW (lower group)
• = mean BW (upper group)
0
139
238
280
330
384
Day of the Experiment

body weights. The last two values for the upper group are the means of four and three animals, one of which weighed 420 Kg at 238 days and 422 Kg at 280 days of the experiment. This animal was almost three times heavier than the other animals in the intermediate upper group at 238 and 280 days thus affecting disproportionately the total mean.

Table 13

Mean Body Weights of the Steers in the Intermediate Group on Each Weighing Date

Day of the Experiment	N	Lower Group	N	Upper Group
		Mean BW		Mean BW
		Kilograms[a]		
0	7	158.3 ± 34.8	12	204.9 ± 88.0
139	4	133.8 ± 14.3	8	196.3 ± 90.8
238	2	149.0 ± 10.2	4	213.3 ± 124.6
280	2	147.5 ± 16.3	3	242.0 ± 155.9
330	2	146.5 ± 14.8	0	----
384	0	----	0	----

[a]All numbers are mean body weights ± standard deviation.

N = Number of animals

The means of the intermediate group in both treatments were significantly lower than the mean body weights of the final group at all stages of the experiment. The influence of the low body weights of the intermediate group on the means of all animals can be seen in Table 12. The means of all animals are lower than those of the final group at all stages, except at 384 days when the steers remaining consisted of only those in the final group.

Summary of Mean Body Weight Data: An inspection of the mean body weight data revealed some distinct features. First, the final group of steers increased their mean body weight at each subsequent weighing period. Second, the difference of mean body weights between the lower and upper groups was not significant at any of the weighings. Third, the initial mean body weights for each treatment were notably higher in the final group than those for all steers. This was primarily the result of the loss of smaller animals; survival favored the larger steers.

Total and Average Daily Body Weight Gains: The data of Tables 14 and 15 were calculated using the mean body weights of Tables 11 and 12 and the number of days in each period (Table 10). Changes in total and average daily gains (ADG) are proportional because ADG was computed by dividing the increase of body weight during each period by the number of days in the respective period.

Table 14

Total and Average Daily Body Weight Gains per Animal of the Final Group of Steers During Each Period

Period	Days in Period	Total BW Gain (Kg)		Average Daily BW Gain (gm)	
		Lower Group	Upper Group	Lower Group	Upper Group
I	139	1.2	6.3	8.6	45.3
II	99	24.5	8.3	247.5	83.8
III	42	1.8	0.8	42.9	19.1
IV	50	12.6	18.9	252.0	378.0
V	54	5.5	8.9	101.9	164.8
I-V	384	45.6	43.2	118.8	112.5

Table 15

Total and Average Daily Body Weight Gains per Animal of All Steers Remaining During Each Period

Period	Days in Period	Total BW Gain (Kg)		Average Daily BW Gain (gm)	
		Lower Group	Upper Group	Lower Group	Upper Group
I	139	10.1	10.2	72.7	73.4
II	99	37.3	27.6	376.8	278.8
III	42	1.4	11.7	33.3	278.6
IV	50	11.2	34.4	224.0	688.0
V	54	25.3	8.9	468.5	164.8
I-V	384	85.3	92.8	222.1	241.7

The data of Table 14 reveal the long-term response to high altitude conditions. These steers survived the entire experiment. Although the total body weight gains for the trial were about equal for both the lower and upper groups, the periods of major body weight were unevenly distributed during the year. Individual tolerance of the conditions at both altitudes varied substantially. The initial adjustment to high altitude and the rainy season resulted in very low ADG for period I in both groups. During period II, when lush pasture growth occurred and moderate weather conditions prevailed, the lower group responded well. The upper group was subjected to more severe weather conditions and steeper terrain than the lower group at all stages of the experiment. The colder microclimate of the upper pasture area delayed rapid pasture growth for several months. The plant density of the upper pasture was less than that of the lower pasture throughout the experiment. The lower pasture was rapidly grazed; most of the better forage was consumed during period III. The upper group of steers relied on forage of poorer quality until maximum forage growth had occurred toward the end of period III. The grazing pressure was less in the upper group, due to more land available per animal, which allowed the pasture growth to continue and not become depleted. During period IV the balanced mineral mix was provided to the steers in both groups and resulted in a major increase in total body weight gain which was also seen in period V. The most severe part of the rainy season coincided with period V causing diminished ADG, yet the ADG was significantly greater than that observed during comparable weather conditions of period I. It is evident that mineral supplementation is beneficial for growth even during severe weather.

Summary of Total and Average Daily Body Weight Gains: The measurements of mean body weight and the resultant calculations of ADG were sufficiently sensitive to detect changes in the environment but were not sensitive to the average difference of altitude (1,150 feet) imposed upon the two treatment groups. When adequate amounts of forage were available in both pastures ADG increased, and these changes were modified by the degree of environmental stress. Similar weather conditions occurred during periods I and V. The ADG for period V were from 3.6-11.8 times greater than those in period I. Part of this increase reflects the effect of the steers consuming a balanced mineral mixture during period V. The low gains in period I are the result of an inadequate mineral intake as well as the stress of acclimatization.

The portion of the trial during which the mineral mixture was fed amounted to 27 percent of the total time of the experiment. Yet, during this time the amount of the total gain in body weight for the experiment of the final group of steers was 39.7 percent for the lower group and 64.4 percent for the upper group. The respective values for all steers were 42.7 and 46.7 percent.

The ADG for period I for the final group and all steers was low and accounted for by the stress of acclimatization and severe weather conditions. Assuming that most of the necessary acclimatization had occurred by the end of the first period of 139 days, then acclimatization played a minor role in the following periods. The body weight measurements after period I would reflect the dietary and climatic changes. During the last four periods the final group of steers achieved an average daily gain of 181.2 gm in the lower group and 150.6 gm in the upper group. The respective values for all steers were 306.9 gm and 337.1 gm per day.

Mean Body Weight and Survivability: Table 16 expresses the mean body weights of the final and intermediate groups as a percentage of the total mean body weight at each weighing date. The mean body weights are unevenly distributed, a reflection of an *ex post facto* selection of means based on those animals which survived the experiment. The initial mean body weights of those steers that died during the experiment were

53.8 and 67.4 percent those of the final lower group and final upper group, respectively. This difference increased during the experiment in the lower groups and decreased in the upper groups.

Table 16

Mean Body Weights at Each Weighing of Steers in the Final and Intermediate Groups as a Percentage of the Mean Body Weight of All Steers

Day of the Experiment	Lower Group		Upper Group	
	Final	Intermediate	Final	Intermediate
	----------------Percentage----------------			
0	115.6	62.2	119.5	80.5
139	111.6	50.5	117.3	74.1
238	106.0	49.3	109.0	72.9
280	106.1	48.6	105.1	79.6
330	106.3	46.6	100.0	--
384	100.0	--	100.0	--

<u>Discussion of Body Weight Data</u>: The lower and upper groups of steers were selected according to body weight and had equal mean body weights of 254.6 Kg. The range of body weights was 125-426 Kg in the lower group and 129-426 Kg in the upper group. The medians were 238.5 Kg and 230.0 Kg, respectively.

Multiple regression analyses of mean body weights and days of the experiment were performed on the following combinations of data: (1) the lower and upper groups before and after mineral supplementation; (2) the lower and upper groups for the entire experiment; (3) the lower and upper groups combined before and after mineral supplementation; and (4) the lower and upper groups combined for the entire experiment.

Regression analysis confirmed the increases of mean body weights before and after mineral supplementation. The rates of gain of both the lower and upper groups were significantly greater ($P < .05$) during the period of mineral supplementation compared with the period of no supplementation. The rates of gain for both groups during mineral feeding were also significantly greater than during a comparable period of severe weather when minerals were not fed. The period of mineral supplementation occurred during the final 104 days of the 384-day trial.

The regression coefficients for mean body weights before and after mineral supplementation (intercept) were, respectively: lower group = 290.2 kg and 277.3 kg; upper group = 303.7 kg and 251.0 kg. The regression coefficients for days of the experiment (slope) before and after mineral supplementation were, respectively: lower group = 0.105 and 0.164; upper group = 0.059 and 0.253. The variance of mean body weights at each stage of the experiment for both the lower and upper groups was larger during mineral supplementation than during the period when minerals, except for trace elements, were not fed to the cattle.

The trial was established with the knowledge that a loss of animals might occur. The interpretation of the data would be easier had no animals died or had the loss been equal in both groups. The mortality is of interest, however, because there were factors causing death in addition to diet quality and quantity. Improvements in management practices made a substantial impact on the reduction of animal losses.

The stress of high altitude on animal production is shown in both treatment groups and was more severe at the higher altitude. The upper group gained less body weight than the lower group and suffered greater mortality. The data suggest that the smaller animals were less able to withstand the rigors of the experimental conditions. Absolute body weight gains and the percentage gain from the initial values were lower for the smaller animals compared with the larger steers. Although this is typical of gains in normal conditions, these measurements for nonsurvivors compared with the survivors were below normal.

Some of the larger steers were close to a typical market weight at the beginning of the trial yet were able to increase their body weight in spite of the poor quality of forage available to them. In Table 17 it can be seen that both groups of all steers gained more than twice the initial body weight compared to the final group.

This response is more a reflection of the low initial body weights of all steers than true body weight gain because most of the nonsurvivors had mean body weights notably below the mean for the group. As steers died the mean body weight of the remaining steers increased by difference.

Table 17

Mean Body Weights at Each Weighing of All Three Groups of Steers as a Percentage of Their Respective Initial Body Weights

Day of Experiment	All Steers		Final Group		Intermediate	
	Lower Group	Upper Group	Lower Group	Upper Group	Lower Group	Upper Group
0	100.0	100.0	100.0	100.0	100.0	100.0
139	104.0	104.0	100.4	102.1	84.5	95.8
238	118.6	114.8	108.7	104.8	94.1	104.1
280	119.2	119.4	109.3	105.1	93.2	118.1
330	123.6	133.0	113.6	111.3	92.5	--
384	133.5	136.4	115.5	114.2	--	--

The relevant data, those data not confounded by changes in group size, are those for the final group at each stage of the experiment. The measures of body weight were sensitive to experimental and environmental conditions. Acclimatization during the rainy season, poor gains during the dry season and accelerated body weight gains during the period of mineral feeding are factors which need to be considered in the interpretation of the data. There were three major aspects which had not been previously determined experimentally in Ecuador. First, Holstein steers can gain weight under conditions of altitude up to 13,800 feet, in spite of severe weather and poor forage. In the economic climate of Ecuador, body weight gains comparable to those recorded in the trial may be profitable. Second, mineral supplementation can increase appreciably the growth rate. Third, the mortality rate is high but can be reduced through good management. It is probable that death losses can be decreased by implementing an adequate nutritional program prior to sending young steers to the *páramo*.

Summary of Body Weight Measurements: A summary of the body weight measurements is presented in Table 18. The data for both the lower and upper groups have been combined in this table because one-way analysis of variance indicated no significant differences between these groups in body weight due to altitude at any stage of the experiment. Table 18 presents the body weight data for all steers and the final group in the periods before and after supplementation of the diet with a balanced mineral mixture and for the entire experiment. At first glance, the data for all steers in each period compared to the final group indicates that there was a greater rate of gain achieved by "all steers." The data are misleading because the final group was established by including only those steers that survived the

Table 18

Summary of Body Weights and Changes in Body Weight of the Final Group and All Steers (Lower and Upper Groups Combined)

Measurement	All Steers	Final Group
Number of Animals	29-48	29
<u>Before Mineral Feeding</u>:		
Beginning BW	254.6 Kg	298.4 Kg
Final BW	303.7 Kg	320.9 Kg
Mean Change in BW	49.1 Kg	22.5 Kg
Percentage Change in BW	19.2 %	7.5 %
ADG	175.4 gm	80.4 gm
<u>After Mineral Feeding</u>:		
Beginning BW	303.7 Kg	320.9 Kg
Final BW	343.0 Kg	343.0 Kg
Change in BW	39.3 Kg	22.1 Kg
Percentage Change in BW	12.9 %	6.9 %
ADG	377.9 gm	212.5 gm
<u>Total Experiment</u>:		
Initial BW	254.6 Kg	298.4 Kg
Final BW	343.0 Kg	343.0 Kg
Change in BW	88.4 Kg	44.6 Kg
Percentage Change in BW	34.7 %	14.9 %
ADG	230.2 gm	116.1 gm

experiment, and their mean body weight notably increased due to the deaths of smaller animals. The mean body weights of the nonsurvivors were low which caused the initial mean body weight of all steers to be more than forty-three kilograms below that of the final group.

The effect of mineral supplementation on body weight gain was clearly demonstrated in both groups. Although ADG was lower for the final group in all periods, the ADG in the final group was 164 percent higher after minerals had been fed, whereas the increase in ADG for all steers was only 115 percent.

Age

The average ages of animals by treatment and analytical category are presented in Table 19. The average age of the final group was higher than that for all steers and the intermediate group. These data illustrate the loss of younger animals. When a younger animal died, the average age of the remaining steers increased.

The simple correlations of age and body weight at each weighing in the original group of forty-eight steers and in the final group are shown in Table 20. The correlations were high in the final group throughout the experiment, although slightly lower toward the end of the trial. There were no significant differences between the upper and lower groups. These data suggest

Table 19

Average Age of Steers on Each Sampling Date for Each Treatment and Analytical Group

Day of Trial	Lower Group			Upper Group		
	All Steers	Final	Inter-mediate	All Steers	Final	Inter-mediate
	Days					
0	454	521	290	453	521	354
139	611	660	401	604	660	520
238	736	759	539	728	759	634
280	778	801	581	785	801	722
330	828	851	631	851	851	---
384	---	905	---	---	905	---

Table 20

The Simple Correlations (r) of Age Versus Body Weight in the Final Group and in All Steers

Day of Trial	Final Group		All Steers	
	Lower Group	Upper Group	Lower Group	Upper Group
0	.85	.86	.90	.91
139	.89	.88	.92	.91
238	.87	.88	.88	.92
280	.84	.86	.86	.91
330	.81	.85	.83	.85
384	.80	.82	.80	.82

that the steers in this trial were similar to cattle in other countries because age and body weight usually are highly correlated. A low correlation would indicate that poor nutrition or management was detrimental to normal growth rate.

Animal Mortality

A major aspect of the experiment was the high mortality rate. The causes of death were divided into two general categories. One category included deaths from disease or other metabolic disorders. The other type of death, physical or traumatic, was caused either from the steers falling off the high cliff on the southern edge of the experimental site or by falling into the deep ditch on the northern perimeter. The causes and dates of death in both the lower and upper groups are listed in Table 21.

The diagnoses made by the INIAP veterinarians on the animals that died as a result of disease or metabolic disorders were imprecise. The diagnoses of the nine steers that died from "pneumonia" were based on the presence, at autopsy, of excess pulmonary and bronchial edema. Respiratory difficulties were observed prior to death of these animals and in others that did not succumb. Penicillin treatment of steers showing signs of pneumonia was only moderately successful in preventing death. Rectal temperatures

Table 21

Date and Causes of Death of Steers at Both Altitudes

Date of Death	Group	Cause of Death
2/26/73	Upper	Pneumonia, diarrhea
4/4/73	Upper	Fell off cliff
4/11/73	Lower	Fell into deep ditch
4/12/73	Lower	Fell off cliff
4/19/73	Lower	Pneumonia, parasites
5/4/73	Upper	Fell into deep ditch
7/10/73	Upper	Fell off cliff
7/16/73	Upper	Fell into deep ditch
8/6/73	Upper	Fell into deep ditch
9/21/73	Lower	Pneumonia, parasites
9/23/73	Upper	Fell into deep ditch
9/29/73	Lower	Pneumonia, parasites
10/15/73	Upper	Pneumonia
11/19/73	Upper	Possible spider bite, (no apparent cause)
12/23/73	Upper	Fell off cliff
1/1/74	Upper	Pneumonia, possible spider bite
1/7/74	Upper	Pneumonia, diarrhea
2/7/74	Lower	Pneumonia, impacted intestinal contents
3/9/74	Lower	Pneumonia, impacted intestinal contents

were only slightly elevated in these animals, while the respiratory and pulse rates were often well above normal. Respiratory difficulty and pulmonary congestion may have been related more to mild brisket disease than to classical pneumonia. Post-mortem examinations usually revealed a notable cardiac hypertrophy, but only mild edema in the throat and brisket area.

The other principal disease symptoms were more easily diagnosed, yet it was difficult to determine if they were directly causal in the deaths. The first animal that died showed excessive diarrhea and associated lethargy prior to death. However, several animals had diarrhea periodically during the experiment, yet they survived this stress. Two animals were infested heavily with lice. DDT treatment eliminated the lice and subsequent infestations did not occur. Apparently, the steers brought the lice to the páramo from the main research facility. Three additional animals were diagnosed as having internal parasite infestations sufficiently severe to cause or predispose death. At lower altitudes lungworm is a serious problem in younger animals and the steers may have brought mild infestations with them that may have played a role in the pulmonary congestion, but no certain diagnosis was made. Septicemia may have occurred to some extent but was not diagnosable at the experiment station. The two deaths that were attributed to a possible spider bite may have occurred for this reason because the animals appeared to be unaffected by other causes. There is a highly poisonous spider resident in the *páramo*, known to cause death in humans as well as animals. Both of the animals were maintaining body weight prior to death, and one animal was the largest of all the animals that died in the trial. Both animals appeared healthy on the day before death. There is a possibility, though remote, that the two steers were poisoned by consuming an excess of minerals, but death occurred thirty-two days after mineral feeding began, a sufficient period of adjustment to the minerals. Two animals contained impacted, dry ingesta in the rumen and lower gastrointestinal tract. It was difficult for them to rise from the ground and graze. Both steers had distended rumens. The gas pressure was relieved by rumen puncture with an 11-guage needle. This temporary relief was of little benefit. A laxative administered as a drench did not relieve the constipation.

The cumulative total deaths by cause of death and by day of the experiment are presented in Figures 4, 5 and 6. The major events of the experiment shown in Figure 4 may have been related to mortality. The fence construction definitely reduced the number of deaths from physical causes.

Fig. 4. Cumulative Loss of Animals in Both Groups by Cause of Death and Day of the Experiment

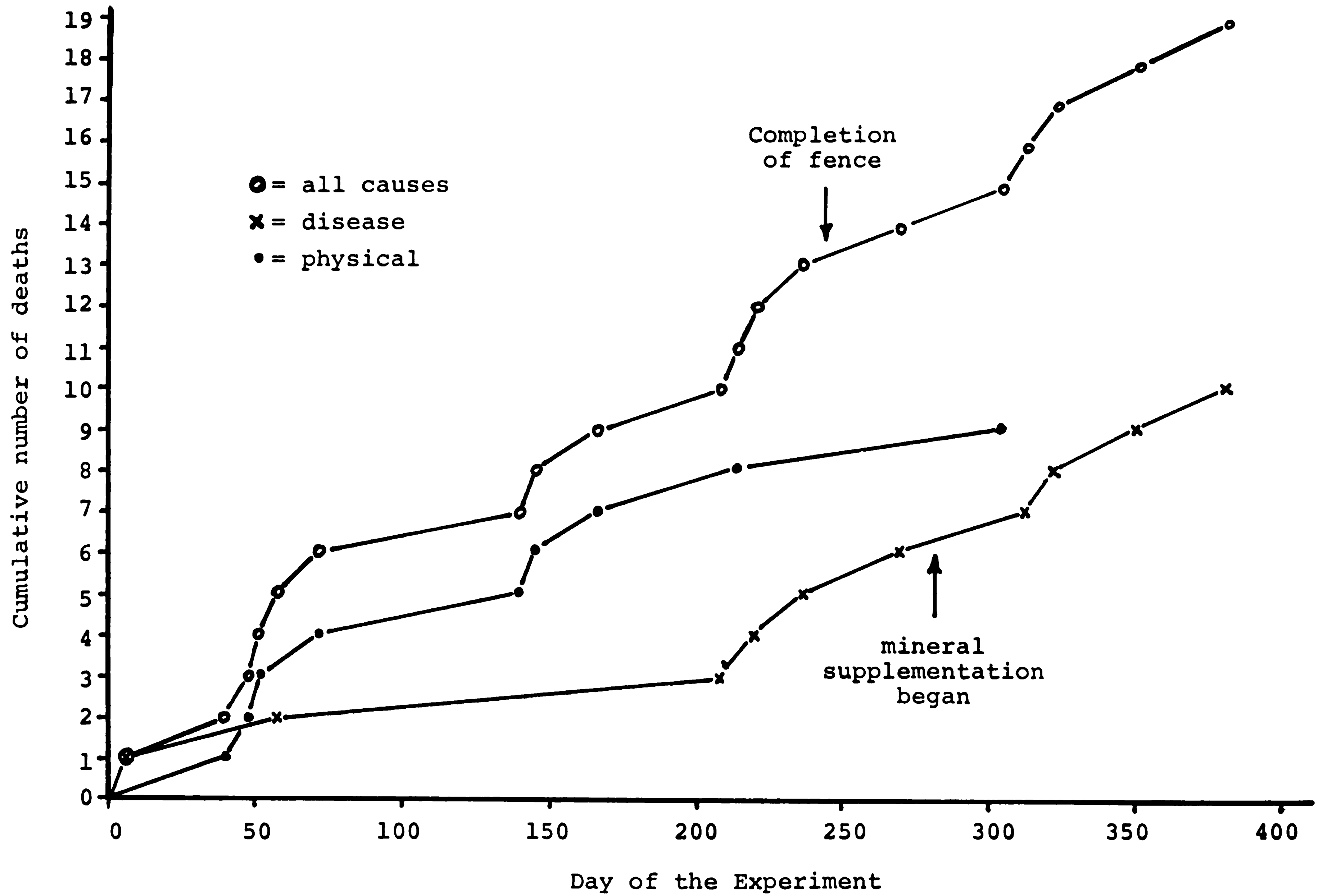

Cumulative number of deaths
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
= all causes
= disease
= physical
Completion
of fence
mineral
supplementation
began
0
50
100
150
200
250
300
350
400
Day of the Experiment

Fig. 5. Cumulative Loss of Animals in the Upper Group by Cause of Death and Day of the Experiment

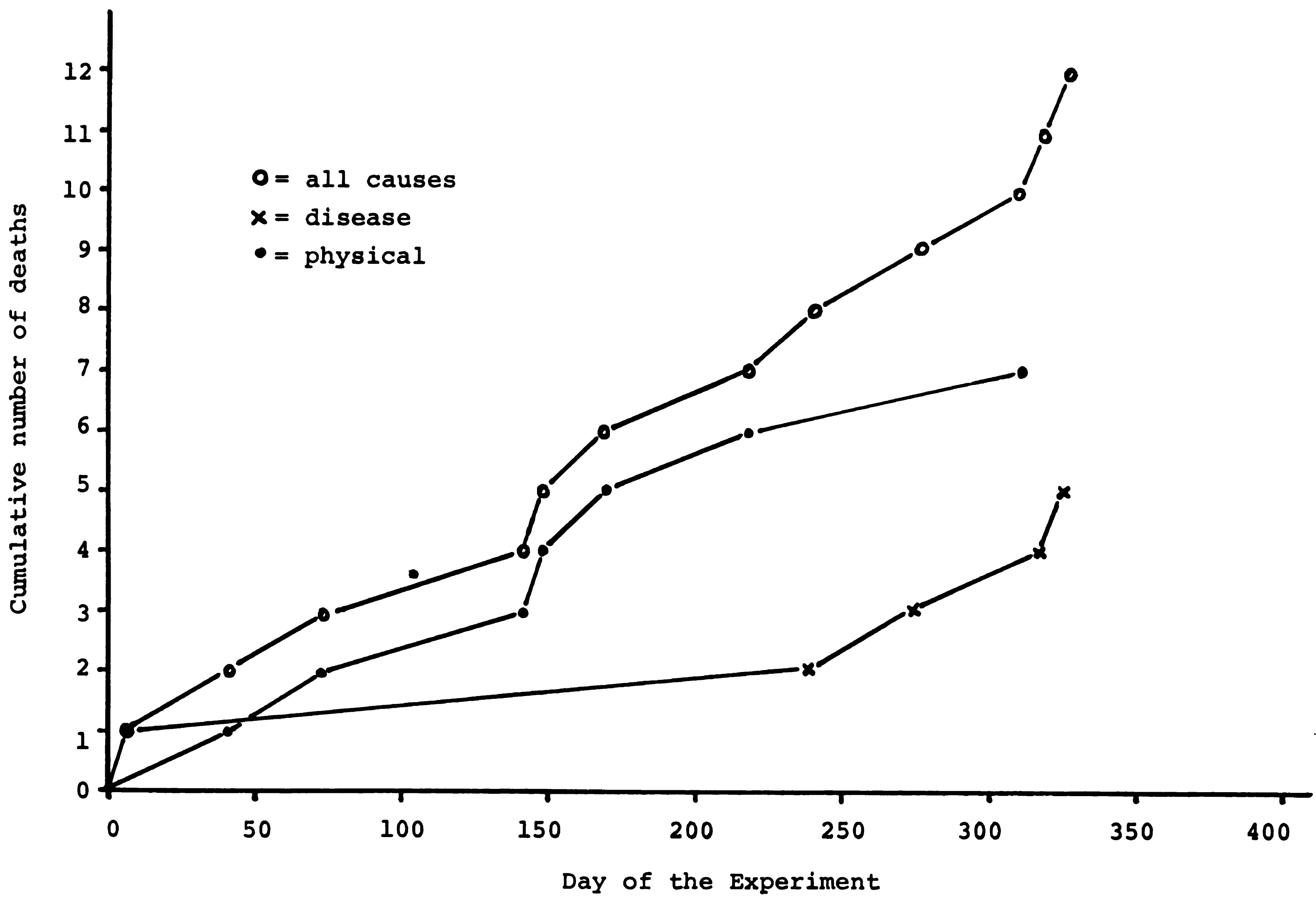
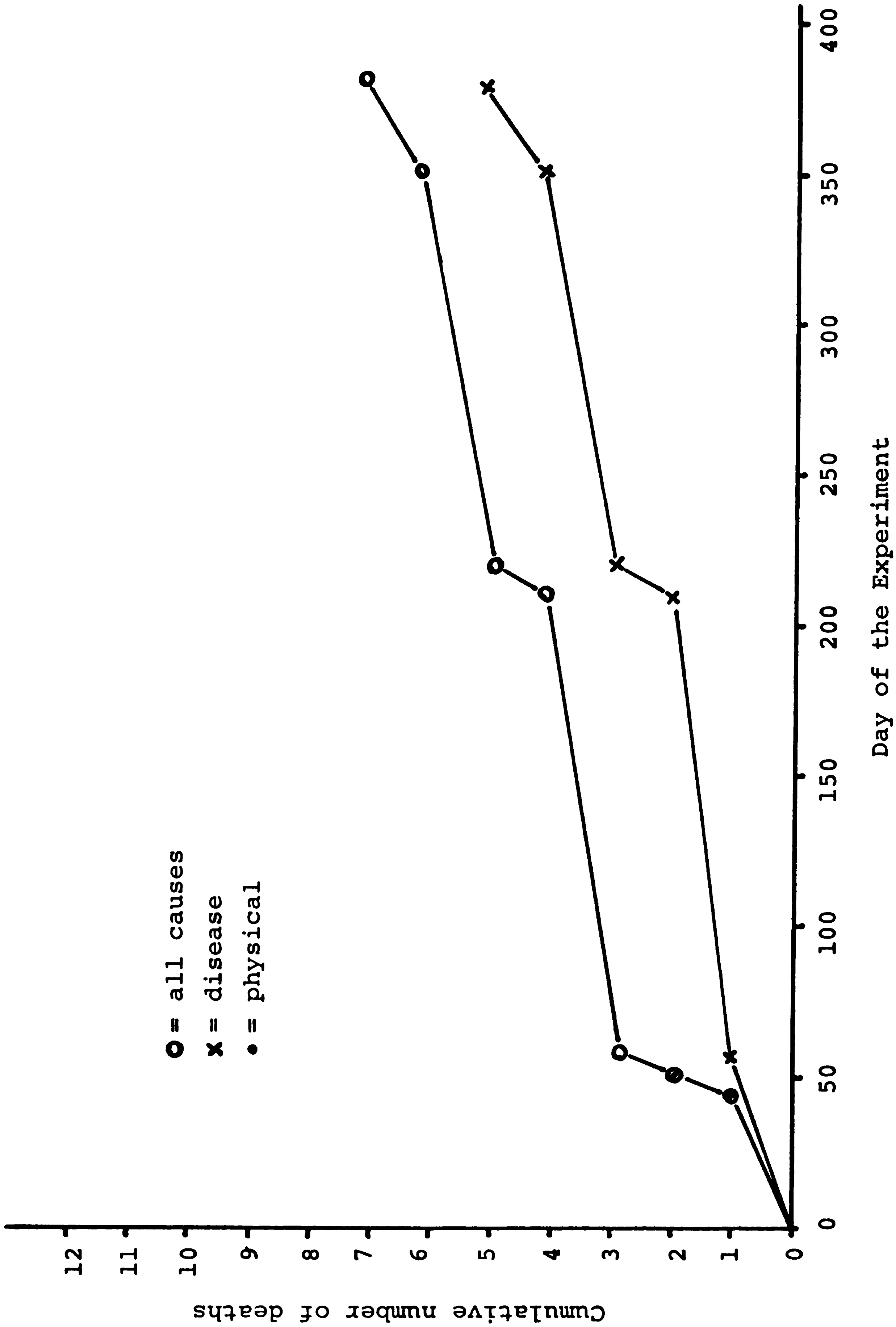

o = all causes
x = disease
• = physical
Cumulative number of deaths
0
1
2
3
4
5
6
7
8
9
10
11
12
0
50
100
150
200
250
300
350
400
Day of the Experiment

Fig. 6. Cumulative Loss of Animals in the Lower Group by Cause of Death and Day of the Experiment


O = all causes
x = disease
• = physical
Cumulative number of deaths
0
1
2
3
4
5
6
7
8
9
10
11
12
Day of the Experiment
0
50
100
150
200
250
300
350
400

There were nine deaths attributed to physical or traumatic causes, either from falling over the cliff or into a deep ditch. Four of these deaths occurred below the cliff. Three other animals slipped down in an area of the cliff that was less steep, but were prevented from plummeting the full distance by sliding into an irrigation trench having a depth of about three feet. This also occurred once to the author during the process of extricating one of the steers from this trench. All three animals survived and gained weight, although one of them subsequently died of pneumonia on April 19, 1973. The five deaths following falls into the deep ditch were due to a broken neck and consequent destruction of the spinal cord, to suffocation caused by severe bending and pressure in the neck, or due to a combination of both causes. Several animals survived after falling into the ditch because they landed in a position which did not cause severe distortion of the neck. None of these animals were able to extricate themselves. Several workers were required to remove them from the ditch. None of the post-mortem examinations revealed displaced abomasums, which could have predisposed death from digestive disorders at a later time.

Apparently the animals fell off the cliff or into the ditch while they were grazing. Several steers were observed grazing near the cliff and continued to graze as they moved downward on the increasingly steep area. Those steers that fell must have grazed themselves beyond a point where they could maintain their footing. The other steers fell into the ditch either as they grazed or while trying to jump across it. In the former situation, much of the opening of the ditch along its length was covered with small brush, to an extent that made it difficult to know where the pasture ended and the ditch began. There were some small spaces where the ditch was discernible and animals tried to jump it. Some steers were able to jump across the ditch, whereas others either died or survived the fall. Those that died landed head-first in the bottom of the ditch, indicating they must have grazed their way into it. The steers that survived the fall were usually on their backs when discovered, indicating that they attempted to jump and nearly reach the other side, but slipped backward and slid to the bottom of the ditch. Surprisingly, none of the survivors broke their legs or pelvis. After a gentle slope had been dug to where they had fallen, they were righted and able to walk out on their own.

There were seven deaths from falls in the upper group and only two in the lower group, whereas the mortality due to disease was evenly divided between the lower and upper groups. The length of the cliff exposed to the steers was about twice as great for the lower group, yet only one steer in the lower group died by falling over the cliff compared to three in the upper group. One steer in the lower group died in the ditch compared with the same demise for four steers in the upper group. The length of the ditch exposed to the upper group was nearly twice that of the lower pasture. All deaths from physical causes occurred during the night when visibility was poor and the herdsman was not watching the steers.

During the first three months of the experiment heavy rains prevented the building of fences to reduce losses from falling. The loss of the first steer from a fall over the cliff occurred on the forty-second day of the trial. By the end of the rainy season, four steers died, two by falling off the cliff and two in the ditch. The need for extensive fence installation was recognized early in the trial and, after lengthy negotiation, the materials were received and fence-building began in late August, 1973. A period of nearly seven weeks was required to install an adequate fenceline in the critical areas. One steer of the upper group died during the period of fence construction and only one animal died from a fall over the cliff after the fence was installed. Six of the ten deaths due to disease occurred during the rainy season.

The mean body weights of all animals that died before the end of the experiment are shown in Table 22. This is the "intermediate" group of steers and the data illustrate that smaller, rather than larger animals, were more susceptible to death. Six steers died before a second body weight measurement could be made, therefore no change in body weight could be calculated. One steer died the night following the first weighing of the second weighing period, providing only a single observation. This steer plus the remaining twelve steers survived long enough to calculate average daily gain prior to death. There were small differences in ADG and the absolute values are too small to indicate that significant changes in body weight occurred prior to death, regardless of the cause.

Table 22

Mean Initial Body Weights and Average Daily Body Weight Change Prior to Death of Steers Not Surviving the Experiment

Cause of Death	Mean Initial BW (Kg)		Average Daily BW Change (gm)	
	Lower Group	Upper Group	Lower Group	Upper Group
Disease	159 (5)[a]	198 (5)	-9.5 (4)	1.7 (4)
Falling	157 (2)	210 (7)	---- (0)	-5.5 (5)

[a]Figures in parentheses are the number of steers in each category.

In summarizing the mortality encountered in this experiment several factors are evident. The number of deaths due to disease was the same at both altitudes. Although the lengths of the cliff and the ditch to which the steers were initially exposed were about equal in both pastures, many more steers in the upper group died from falls than in the lower group. The deaths of all animals regardless of cause occurred in a period of 376 days of a possible 384 days, an average of one death approximately each twenty days. The deaths from all causes were grouped into four distinct periods (Figure 4). Eight of the nine deaths due to falls occurred before fencing was completed. Six of ten deaths due to disease occurred during the rainy season, whereas the remaining four fatalities occurred during a two-month period in the latter half of the dry season. It must be remembered that the "dry season" is a relative term because conditions in the *páramo* remain cold and damp during this time. Precipitation continues but is less than during the rainy season. In addition, the winds are very strong during the dry season which adds to the stress on the livestock grazing there. Another feature of the data is the greater mean body weight of the animals that died from falls versus those due to disease. The larger animals were more aggressive while grazing and tended to graze a larger area than did the smaller steers.

It is evident from the data that the management of animals in the conditions of this experiment must include adequate fencing and supervision of livestock movement. In addition, rigorous health measures must be employed for the prevention, early diagnosis and the cure of disease. A major observation was the absence of severe brisket disease. There was some gross evidence of edema and jugular vein pulsing, but these symptoms were never severe and none of the animals displayed all of the symptoms of even moderate brisket disease. It may be that the disorder is debilitating, and perhaps fatally predisposing, in Ecuador, but the classical symptoms probably are not sufficient for early diagnosis of the disease. To the extent that it was observed in this trial, brisket disease is not a major deterrent to the utilization of the *páramo* for meat production using the male Holstein.

Hematocrit

The mean hematocrit values for all analytical groups of steers and fifteen "control" animals are presented in Table 23. The control animals were milking cattle and yearling heifers which were raised and maintained at 10,000 feet of altitude, the elevation of the Dairy Research Center. Control samples of the steers were not taken before the beginning of the trial because of a lack of sampling equipment.

Table 23

Mean Hematocrit Values of Fifteen Control Animals and Steers in Three Analytical Categories

Day of Experiment	Control Group	Final Group		All Steers		Intermediate Group	
		Lower Group	Upper Group	Lower Group	Upper Group	Lower Group	Upper Group
	percentage packed-cell volume[a]						
--	39.4 ± 3.1	--	--	--	--	--	--
139	--	40.9 ± 4.2[b]	41.0 ± 3.2[b]	40.5 ± 4.1[b]	41.0 ± 3.6[b]	38.7 ± 3.3	41.0 ± 4.3
238	--	43.9 ± 4.7[c]	44.9 ± 4.9[c]	43.4 ± 4.7[c]	45.2 ± 4.6[c]	39.2 ± 1.8	46.2 ± 3.9
384	--	50.4 ± 8.7[b,c]	49.5 ± 9.0[b,c]	50.4 ± 8.7[b,c]	49.5 ± 9.0[b,c]	--	--

[a]All values are means ± standard deviation.

[b]Means sharing same superscripts within a column are significantly different ($P < .005$).

[c]Means sharing same superscripts within a column are significantly different ($P < .05$).

The normal hematocrit (packed cell volume) range of mature bovines (Bos taurus) is 30.3-34.9 ml/100 ml blood with a mean value of 32.4 m./100 ml blood (55). The hematocrit usually declines with age in low altitude conditions. The hematocrit value of the control group was higher than that of sea level conditions (55) suggesting that an adjustment to 10,000 feet of altitude includes elevation of the hematocrit which is maintained during exposure to this elevation. All groups showed a significant increase in hematocrit during the experiment. The changes in hematocrit of the steers in the final group were significant for each period. There were no significant differences between the treatment groups on each sampling date although the mean hematocrit value of the upper group was consistently higher. This suggests that the measurement of hematocrit was not sufficiently sensitive to detect differences due an average altitude increment of 1,150 feet between the two groups.

Under normal altitude conditions the hematocrit tends to decline as age increases, being highest in the first weeks after birth in the bovine. In addition, the hematocrit increases after initial exposure to altitude regardless of age, then stabilizes at a level higher than that at the lower level after a few weeks of exposure. Neither of these phenomena occurred in this trial. Age and hematocrit were positively correlated at each sampling of the upper group and at the last sampling of the lower group (Table 24). The slightly negative correlations on the first two samplings of the lower group became positive at the end of the trial suggesting that hematocrit was increasing as rapidly as age. The mean hematocrit steadily increased throughout the trial rather than stabilizing after acclimatization was complete. The change in hematocrit during each period for both groups was closely related with the number of days in each period. The data suggest that the change in hematocrit was fairly constant throughout the trial and had not begun to stabilize by the end of the experiment.

Table 24

The Simple Correlations (r) of Hematocrit Versus Age in the Final Group of Steers

Sample Date	Lower Group	Upper Group
July 10, 1973	-.29	.51
Oct. 17, 1973	-.02	.31
Mar. 12, 1974	.07	.49

The body weight data indicated that survivability favored the heavier animals which, under normal experimental conditions, should have resulted in lower mean hematocrit values than those observed, due to a normal decline in hematocrit with age. This interaction should have resulted, at least, in no change of mean hematocrit during the trial, and might have yielded a decline during each period.

The blood samples of the steers after 139 days of adjustment to higher altitudes yielded a small increase in the mean hematocrit of both groups compared to the control value. After 238 days there was a significant elevation of the hematocrit which may be accounted for, in part, by continuing stress. The rise in packed-cell volume between the second and third samplings, however, indicates there must be other factors operative in the polycythemia, because there is a limit to which the hematocrit can increase without deleterious effects. These effects include excess viscosity and osmolarity which could alter the normal processes of metabolism, electrolyte exchange and oxygen diffusion to the tissues. The increase in hematocrit between the first and second samplings, when an unbalanced mineral mixture was irregularly offered, was significant for both treatment groups and changed at a rate of 0.034 percentage units daily. The hematocrit increased by 0.039 percentage units per day from the second to the third sampling. This daily increase of hematocrit was 13.4 percent greater than during the first period. The accelerated increase occurred at a time when it would be expected that hematocrit should have stabilized. This period corresponds to the time when the balanced mineral mixture was regularly offered. Perhaps this mixture caused some of the increased erythropoiesis by providing necessary erythropoietic nutrients. Another explanation could be that excessive mineral intake increased the osmolarity or viscosity of the blood. The metabolic benefit to the animal of continued increases in erythrocytes was not explained by the body weight data, because increases in average daily gain were not proportional to the change in hematocrit. It is not suggested that ADG is highly correlated with hematocrit values but low hematocrit could limit metabolic efficiency. The continued increase in hematocrit was due, only to a small extent, to the need for more oxygen to support body weight gains.

A principal question concerns the exaggerated increase in hematocrit at a time when lower values than those measured in the trial, and stabilized levels, would be expected. Polycythemia can occur directly through stimulation of erythropoiesis and from the early and transient release of red blood cells from splenic storage in response to hypoxia. It can occur indirectly by a loss of blood water, blood serum or plasma which results in a net decrease of blood volume and a consequent increase in red blood cell volume per unit of extracellular blood fluid. Total blood and blood fluid volumes were not measured in this trial. A change in this component may have occurred contributing to the elevation of hematocrit. It is not known whether a change in blood fluid volumes could occur sufficiently, without metabolic detriment, to be the primary cause of such high hematocrit values.

The continued increase of the number of red blood cells indicates the need for elevated oxygen transport, exceeding the increase normally expected at the altitudes included in the experiment. Perhaps there was a direct stimulation of red blood cell production, or indirectly there may have been toxic factors that excessively blocked oxygen-binding by hemoglobin. Additionally, oxygen transport across the pulmonary system may have been reduced, or oxygen uptake may have been partially inhibited.

Blood Minerals

The concentrations of macroelements and microelements in blood are often used as indicators of the mineral status of the organism under study. In many instances, assuming the human or animal is not under severe stress, these values can aid in the assessment of mineral status. Changes in blood mineral concentration related to dietary treatment offer insight into the mineral status of the organism under investigation. However, at best, the sampling of a single tissue or blood can rarely provide a complete understanding of the mineral status. Complete mineral status can only be determined by measuring the minerals in other tissues and in the diet. This is a costly method requiring the study to focus more on mineral status and less on the practical aspects of production.

This trial was designed to obtain some perspective of the mineral status of steers subjected to high altitude stress and poor quality feeds, to the extent that analysis of minerals in a single body component, blood, could provide basic information. Serum mineral concentrations are a classical measure in the research literature and permit some comparison of the values measured in this trial with data compiled under "normal conditions." However, just as the values in one tissue limit the assessment of mineral status, so does the lack of previous information on the mineral content of feeds, water and animal tissues at high altitude in Ecuador reduce the ability to understand completely the mineral metabolism of the experimental stresses.

This section of results will discuss blood mineral concentrations and how they compare with mineral levels determined in countries other than Ecuador, but in similar production situations. Altitude is a factor of this trial which is not a variable affecting the analyses from other locations. Little information exists on serum mineral levels in bovines at high altitude. The effects of altitude on mineral requirements have not been established. Normal, sea-level values for some serum minerals also may be "normal" at altitude but the stress of the environment and hypoxia may increase the requirements for other minerals. A high serum mineral value at altitude, compared with the "normal" concentration at sea level, may indicate that the requirement for the circulating or mobilized mineral is higher than at sea level, or storage may be inhibited as a consequence of the diet or environment. A low serum mineral value may be "normal" at altitude because of increased uptake by the tissues or due to a true deficiency in the diet. These concepts illustrate some of the difficulty in interpretation of the blood mineral content of animals in conditions for which few data exist on mineral levels and requirements.

Serum Calcium Concentration: The serum calcium contents in all analytical categories are presented in Table 25. Of most interest are the serum calcium values for the final group of steers. The treatment differences due to altitude were not significant in any analytical category for any of the three sampling times as determined by analysis of variance. As the experiment proceeded, there was a decline in serum calcium concentration which was most pronounced in the lower group but none

Table 25

Serum Calcium and Magnesium Concentrations by Analytical Category and Treatment Group

Date of Experiment	Serum Calcium Concentration		Serum Magnesium Concentration	
	Lower Group	Upper Group	Lower Group	Upper Group
	ppm			
Final Group				
139	89.2 ± 10.1[a]	89.1 ± 11.2	27.69 ± 2.4[b]	28.14 ± 3.3[b]
238	86.5 ± 11.9	88.6 ± 12.0	27.85 ± 3.8[c]	29.79 ± 3.5[c]
384	85.9 ± 10.4	88.4 ± 13.5	22.91 ± 3.2[b,c]	24.51 ± 2.9[b,c]
All Steers				
139	88.4 ± 10.9	83.6 ± 11.5	27.28 ± 2.7[d]	27.72 ± 2.7[d]
238	85.7 ± 11.5	85.6 ± 11.8	27.42 ± 3.8[e]	28.81 ± 3.7[e]
384	85.9 ± 10.4	88.4 ± 13.5	22.91 ± 3.2[d,e]	24.51 ± 2.9[d,e]
Intermediate Group				
139	85.0 ± 15.2	79.8 ± 11.5	25.56 ± 3.8	27.10 ± 1.2
238	79.0 ± 2.5	76.6 ± 5.4	23.77 ± 0.3	25.86 ± 2.9
384	----	----	----	----

[a]All figures are means ± standard deviation.

[b,c,d,e]Means in a column sharing the same superscript are significantly different ($P < .01$)

of the measurements were statistically significant. Normal serum calcium concentration is in the range of 90-120 ppm in the bovine (55). The values measured in this trial ranged from 59.9-112.4 ppm with an overall mean of 86.2 ppm. Because the mean was below the normal range and the forage contained less than one-half of the requirement, the mineral supplement included an adequate supply of calcium in the form of steamed bone meal. The supplementation began after the second sampling, but appeared to have no beneficial effect on raising the serum calcium to normal levels.

Calcium is essential for bone growth, blood clotting, cardiac function, enzyme activation and membrane permeability. Severe calcium deficiency can retard skeletal development and reduce growth. Combined with a phosphorus deficiency, a low intake of calcium can cause weak bones with consequent fracturing, stiff joints and lameness. Lameness can diminish growth by reducing appetite and restricting the movement necessary for grazing.

Forage and soil levels of phosphorus were low in the experimental area. The forage phosphorus level was only one-fifth the requirement for growing steers (199). The calcium deficiency in the forage, combined with the severe phosphorus shortage and the reduced dry matter intake aggravated the calcium:phosphorus relationship and produced a severe deficiency of both minerals. The need for supplemental calcium and phosphorus exists in the best animal production systems except where the major portion of the dry matter intake is satisfied with high quality legumes. It is evident, because of the deficiencies noted above, and because of the absence of legumes in the *páramo*, that supplementation of calcium and phosphorus is necessary in amounts in excess of those in typical cattle production schemes.

Both calcium and phosphorus are stored in the body. Ninety-nine percent of the calcium and 80 percent of the phosphorus is stored in the skeleton (255). Only a small amount of each mineral is in solution. Therefore, body reserves serve to protect the organism from periods of deprivation of these minerals and permit the maintenance of levels in the blood.

In steers consuming normal amounts of calcium and phosphorus, circulating levels of these minerals would not be expected to change considerably if the animals were deprived of the minerals for a few weeks. The animals in this trial maintained serum calcium below the normal range for the length of the trial. The mineral was supplemented at a level that entirely met the requirement for calcium, regardless of the forage content of the mineral. Surfeit feeding of calcium did not relieve the slight deficiency of the mineral in the blood. It is possible, although unlikely, in the conditions of the trial the need for calcium was below requirements established under more intensive cattle production systems at low altitude. It could be considered further that 86.2 ppm of serum calcium is the "normal" level at the altitudes of the experiment. But, most steers displayed gross signs of skeletal deterioration as the trial progressed. These signs were most evident in the shoulder area where moderate to severe "winging" occurred in steers of all ages and did not appear to be relieved by mineral supplementation. Lameness in the joints and weak backbones were also observed in many animals. The above observations suggest that even with adequate calcium and phosphorus intake the availability of these minerals was low or absorption was partially inhibited. The high fiber content of the forage and/or an unknown compound may have bound a sufficient quantity of the minerals preventing efficient utilization.

The mean serum calcium concentrations of the nonsurvivors were notably lower than those of the steers that survived the experiment. However, four of the twelve nonsurvivors from which blood samples were obtained died from physical causes. It is difficult to relate all types of death in this trial with low serum calcium, but it may have played a predisposing role.

Serum Magnesium Concentration: The results of serum magnesium analysis are presented in Table 25. The serum magnesium levels of all steers and the final group were similar on the first two dates but were notably lower at the third sampling. Preliminary analyses indicated that magnesium levels were above normal. Therefore, no supplemental magnesium was included in the balanced mineral mixture. The normal range of serum magnesium in bovines is 19.4-26.7 ppm with a mean of 21.9 ppm (55). The range of serum magnesium concentrations of this trial was 17.27-36.26 ppm with an overall mean of 26.69 ppm. Only three of 105 determinations were below the minimum normal value of 19.4 ppm, all of which occurred in the lower final group of steers at the last sampling. In addition, fifty-four of the 105 analyses were higher than the maximum normal value of 26.7 ppm, and were divided evenly between the lower and upper groups. The effect of altitude was not significant at any of the times of sampling. There was a statistically significant ($P < .01$) decline in serum magnesium concentration in the lower and upper groups from the first to third and second to third samplings. The serum magnesium content of a male steer at 10,000 feet was 21.0 ppm, which was in the low side of the normal range, but was apparently sufficient for growth.

Magnesium distribution and metabolism in the body is closely associated with calcium and phosphorus levels. The skeleton and teeth contain about 70 percent of the total body magnesium. The remainder is distributed in fluids and soft tissues and is important in enzyme activation and central nervous system function.

According to the results of this trial, none of the steers were severely hypomagnesemic at any stage of the trial, although three steers were slightly below normal at the end of the experiment. Only four steers had serum magnesium values slightly higher at the third sampling than at the second sampling, indicating there was a notable decline of serum magnesium in the other steers at the end of the trial. The nonsurvivors contained lower serum magnesium concentrations than the survivors but the values were above the normal mean. The deaths in the trial were not related to serum magnesium content although, as the experiment progressed, the concentration of serum magnesium declined. It is possible that steers grazing the <u>páramo</u> for a period several months longer than the twelve and one-half months of this experiment may achieve a hypomagnesemic state which could be prevented or cured by magnesium supplementation.

The dietary requirement of bulls for magnesium at low altitude is 0.08 to 0.1 percent of the dry matter. The forage consumed in the experiment had a magnesium content of 0.040-0.056 percent on a dry matter basis. The slow rate of growth of the steers, compared with higher growth rates obtained under ideal conditions, reduced the need for magnesium. The decline of serum magnesium content at the end of the trial, combined with the observation of skeletal degeneration, indicates that magnesium reserves may have become depleted after twelve and one-half months of grazing in the *páramo*. Hypomagnesemia, as a result of consuming *paja de páramo* for a long time, and the hyperexcitability which accompanies low serum magnesium levels, may be masked by the lethargy common at high altitude. Therefore magnesium supplementation may be necessary for steers that are expected to graze in the *páramo* for periods greater than one year. Without supplemental magnesium the steers could reach a point at which magnesium might become a major factor restricting growth.

Serum Sodium Concentration: The serum sodium concentrations in the three analytical categories and two treatment groups are presented in Table 26. With the exception of serum sodium in all steers of the upper group, the sodium concentration was lowest at the end of the trial than on the other two dates, but in all cases sodium was highest on the first sampling date and

Table 26

Serum Sodium and Potassium Concentrations by Analytical Category and Treatment Group

Day of Experiment	Serum Sodium Concentration		Serum Potassium Concentration	
	Lower Group	Upper Group	Lower Group	Upper Group
	ppm			
Final Group				
139	3842.7 ± 591.6[a]	3989.7 ± 673.7	369.7 ± 53.9	380.1 ± 54.1
238	3703.8 ± 296.9	3721.8 ± 353.2	393.5 ± 68.0	391.9 ± 69.9
384	3642.1 ± 397.1	3634.0 ± 206.1	376.5 ± 52.8	379.4 ± 79.9
All Steers				
139	3918.4 ± 559.9[b,c]	3895.4 ± 541.8[b,c]	374.1 ± 52.4	382.9 ± 47.3
238	3673.3 ± 312.1[b]	3584.1 ± 417.5[b]	391.1 ± 65.2	384.9 ± 64.2
384	3642.1 ± 397.1[c]	3634.0 ± 206.1[c]	376.5 ± 52.8	379.4 ± 79.9
Intermediate Group				
139	4240.0 ± 230.4[d]	3754.1 ± 213.1[d]	392.8 ± 47.2	369.9 ± 37.8
238	3413.9 ± 438.6[d]	3171.1 ± 173.9[d]	387.2 ± 39.2	364.0 ± 43.5
384	----	----	----	----

[a]All values are the means ± standard deviation.

[b,d]Means in a column sharing same superscript are significantly different ($P < .01$).

[c]Means in a column sharing same superscript are significantly different ($P < .05$).

significantly greater than subsequent measurements for all steers and in nonsurvivors.

The normal range of serum sodium in bovines is 3,130-3,550 ppm with a mean of 3,300 ppm (55). The range of serum sodium concentrations in the trial was 2,702.5-5,346.9 ppm with an overall mean of 3,741.5 ppm. The wide range of values observed in this trial may be due to the wide range of body weights and ages of the steers. This would reflect variable metabolic needs. In addition, the selection of forages during grazing may also vary with the age of the animal which could notably affect the intake of sodium. The high overall mean of serum sodium concentration suggests that the intake of sodium was sufficient for metabolic needs.

Sodium is involved in the metabolism of water and the control of nutrient uptake by cells. A dietary deficiency causes a loss of appetite, decreased growth, loss of weight and an unthrifty appearance. Although the steers in this trial had depressed appetites, low body weight gains and rough hair coats, the serum sodium levels suggest that these characteristics were not caused by a deficiency of sodium.

The decline of serum sodium concentration during the trial suggests that dietary intake of the mineral was insufficient to maintain previous levels. The steers consumed low quantities of forage, yet the forage sodium content was similar to legumes which are usually higher in sodium than common forage grasses. Even with reduced forage intake the sodium consumption appeared sufficient to maintain adequate blood levels of the mineral.

The serum sodium concentrations for March, 1974 were determined after the steers had received the balanced mineral mixture for 104 days. The mineral supplement had little effect on mean serum sodium levels. The rate of decline of serum sodium concentration in the final group of steers from the first sampling to the second was approximately twice as great in the upper group as compared with the lower group and about 50 percent greater from the second to the third samplings. The daily decline of serum sodium in both the lower and upper group from October, 1973, to March, 1974, was only 30-40 percent of the rate from July to October, 1973. This suggests that either an equilibrium in sodium metabolism was being reached or that the mineral supplement had a positive effect on reducing the rate of decline. It is possible that mineral supplementation permitted the serum sodium levels to approach normal concentrations, making more sodium available for tissue utilization. Inadequate sodium intake early in the trial may have reduced tissue stores of the mineral in favor of maintaining adequate circulating levels. The most definitive conclusion is that sodium status approximated that of sea level steers and there was a sufficiency beneficial for normal metabolism.

The concentration of sodium in the serum of a male Holstein at 10,000 feet of altitude was 6,600 ppm (0.66 percent) and in the whole blood was 6,200 ppm. This value is twice both the normal sea-level value and the concentration in the blood of steers exposed to the two altitudes of this trial. Because of the wide range of serum sodium measured in the trial the high sodium concentration at 10,000 feet of altitude does not indicate that the concentration declines with altitude.

The levels of sodium in the serum of the steers that subsequently died from various causes (Table 26) were variable, yet close to the normal range found at sea level. The data indicate that the deaths of these steers were not closely related to deficient or excessive serum sodium concentrations.

Serum Potassium Concentration: The serum potassium concentrations for the three analytical categories and two treatment groups are presented in Table 26. Serum potassium values were highest at the second sampling for all steers and the final group. There were no significant differences among the serum potassium concentrations. The normal concentration of potassium in bovine blood at sea level ranges from 190-260 ppm with a mean value of 230 ppm (55). The range of values in the trial was 281.3-538.2 ppm, with an overall mean of 381.5 ppm. There were no significant differences due to treatment or with time of the experiment. The mean concentration of potassium in the trial was 65 percent greater than the sea level value.

Potassium is important for cardiac function and the maintenance of osmolarity of body fluids. Potassium deficiency is characterized by retarded growth, emaciation, reduced appetite and decreased digestive efficiency. The body is tolerant of wide ranges of potassium concentration, with sodium partially replacing depleted potassium levels and the kidneys rapidly excreting the mineral when present in excess. Hyperkalemia is often seen during renal insufficiency, alcoholism, low protein intake and negative nitrogen balance.

The hyperkalemia measured in the experiment may result from a combination of factors. These include renal insufficiency due to altitude and/or the low protein content of the principal forage. The forage contained potassium at about one-third of the sea-level requirement of 0.7 percent of the ration dry matter (199), suggesting that the excess serum potassium was not due to high dietary intake of the mineral. There was little effect of mineral supplementation with potassium on serum concentration of the mineral. The concentrations in serum were similar before and after treatment. The mean serum concentration of potassium in the steers that died was equal to that of the survivors, indicating that death was not closely related to serum potassium status.

There are other possible sources of dietary potassium. The steers may have consumed small quantities of other forages that contained high levels of potassium. The water may have contained enough potassium from soil leaching to meet the requirements of the steers for the mineral. The potassium in the mineral supplement was sufficient to meet entirely the dietary requirement.

Serum Iron Concentration: The analyses of blood for serum iron concentration are presented in Table 27. Normal plasma or serum iron content in bovines is in the range of 0.92-2.70 ppm. The range of values in this trial was 6.21-24.07 ppm with an overall mean of 12.35 ppm for all steers and 12.23 ppm in the final group of steers. The mean of nonsurvivors was 12.89 ppm. There were significant differences in total serum iron due to altitude at the time of the first sampling. The highest values were obtained at the second sampling and were significantly greater than the first and third measurements.

Table 27

Concentrations of Serum Iron and Hemoglobin-bound Iron for All Three Analytical Categories

Day of Experiment	Serum Iron: Lower Group	Serum Iron: Upper Group	Hemoglobin Iron: Lower Group	Hemoglobin Iron: Upper Group
	ppm[a]			
Final Group				
139	$13.49 \pm 5.25^{b,c}$	$10.10 \pm 1.93^{b,c}$	370.0 ± 173.3^{c}	$413.4 \pm 117.2^{c,d}$
238	15.09 ± 3.27^{d}	$14.32 \pm 3.10^{c,d}$	331.7 ± 137.4	274.4 ± 137.8^{c}
384	$9.42 \pm 2.14^{c,d}$	10.43 ± 2.36^{d}	279.3 ± 78.6^{c}	287.6 ± 109.3^{d}
All Steers				
139	13.13 ± 4.94^{e}	10.84 ± 3.32^{e}	377.0 ± 171.3^{d}	$433.3 \pm 137.4^{e,f}$
238	15.08 ± 3.10^{f}	$14.48 \pm 3.23^{e,f}$	323.0 ± 132.2	284.3 ± 125.0^{e}
384	$9.42 \pm 2.14^{e,f}$	10.43 ± 2.36^{f}	279.3 ± 78.6^{d}	287.6 ± 109.3^{f}
Intermediate Group				
139	11.62 ± 3.44	11.96 ± 4.66	406.8 ± 184.5	463.1 ± 167.3
238	15.01 ± 1.50	14.96 ± 4.06	249.0 ± 7.5	313.9 ± 83.1
384	----	----	----	----

[a] All values are the means ± standard deviation.

[b] Means in a row sharing same superscript are significantly different ($P < .05$).

[c,d,e,f] Means in a column sharing same superscript are significantly different ($P < .05$).

The absolute values of total serum iron are of interest because they are from two to eight times greater than the upper limit of the normal range. Serum iron normally accounts for 1 to 3 percent of the total iron in the blood and is the transport form of iron in the body. At low altitude the binding capacity of serum transferrin for iron in the male bovine ranges from 33 to 38 percent (254). Thus, the serum has the potential to contain 2.5-3.0 times the normal concentration of serum iron. That the potential binding capacity of serum iron may have been reached in this trial can account only partially for the high levels measured. It is possible that partial hemolysis of the samples occurred during transport and storage, which released hemoglobin-iron from the erythrocytes, and caused an elevation of serum iron.

The serum iron concentration in male steers maintained at 10,000 feet of altitude was in the range of 3.5-4.0 ppm, which is two to three times greater than normal sea level values. Some of the excess serum iron may be attributable to high levels of iron in the soil and for water. The steers could have consumed iron directly from the soil while grazing. The forage was not analyzed for its iron content, but the high serum iron values indicate that it also may have been adequate in iron. It is possible that the steers consumed small quantities of other forage having high iron content.

Concentration of Hemoglobin-bound Iron: The analyses of whole blood for content of hemoglobin-bound iron are presented in Table 27. The decline in concentration of this element bound to hemoglobin was highly significant ($P < .05$) from the first to last measurements in the lower group and from the first to subsequent samplings in the upper group.

The normal range of hemoglobin-bound iron in bovines is 374-408 ppm (55, 75, 184). The hemoglobin of most mammals contains 0.34 percent iron. The hemoglobin content in the blood of bovines is in the range of 11-12 gm/100 ml (55, 75). The range of hemoglobin-bound iron measured in this trial was 99.8-654.7 ppm, with an overall mean of 337.8 ppm. The hemoglobin content of blood rises with altitude. A concurrent rise of iron bound to hemoglobin would be expected. In this trial the hemoglobin-bound iron was slightly below the sea-level value. The iron concentration at the high altitudes of this trial was notably below the expected values. This deficiency, however, may have been compensated for by the extremely high levels of serum iron. Leakage of iron from the red blood cells into the serum may have occurred, accounting for the excess serum iron and for some of the low concentration of hemoglobin-bound iron.

The variability was great within treatments and was not correlated with mortality or body weight gains. Only two of the forty-one steers sampled had hemoglobin-bound iron values that remained above the minimum normal concentration. One of these two steers had normal iron levels at two samplings but died before the last sampling. The mean hemoglobin-bound iron concentration of non-survivors ranged from 33 percent below the lower value of the normal range to 13.5 percent above the upper value of the normal range. Thus, hemoglobin-bound iron status was not correlated with mortality.

The data suggest that several animals may have been marginally iron-deficiency anemic. However, the considerable variability of the body weights and ages of the steers probably accounted for the greater part of the wide range of hemoglobin-bound iron values. The data do not confirm that there was a serious iron-deficiency anemia in steers grazing the <u>páramo</u>.

<u>Summary of Blood Iron Content</u>: The serum iron concentrations of the survivors in the lower and upper groups were significantly different ($P < .05$) after 139 days of exposure to the respective altitudes of the experiment. In addition, mean serum levels in all

animals were notably higher than sea-level values throughout the trial.

The hemoglobin-bound iron concentrations were variable and considerably below sea-level normal levels. The hemoglobin content of the blood would be expected to rise notably due to the need for increased oxygen transport due to the hypoxia of high altitude. Because of the constancy of the iron content in hemoglobin, this is often used as an indicator of hemoglobin status. The low levels of iron bound to hemoglobin in this trial suggest that hemoglobin was not significantly elevated above normal values. However, past research shows a definite increase in hemoglobin in men and animals exposed to high altitude. The expected increase in hemoglobin in this experiment was not detected by the analysis of hemoglobin-bound iron. The data do show that iron-deficiency was not a significant limiting factor for survival and body weight gain.

The relative proportions in the blood of serum and hemoglobin-bound iron were about normal, with the latter being the principal form of iron in the blood of mammals. The correlations between the two forms of iron were relatively high, being highest at the second sampling (Table 28). This is in agreement with the normal relationship of iron distribution in the blood. The high correlations suggest that individual changes in serum iron were proportional to the changes in hemoglobin-bound iron.

Table 28

Simple Correlations (r) Between Serum Iron and Hemoglobin-bound Iron in the Final Group of Steers

Day of Experiment	Lower Group	Upper Group
139	.37[a]	.66
238	.84	.78
384	.60	.51

[a]Correlation coefficient

<u>Concentrations of Other Microelements in Serum</u>: Serum was analyzed for copper, cobalt, manganese, zinc and selenium. The normal serum levels of these microelements are below the minimum level of detection by the analytical instruments that were available. From these analyses it could not be determined with certainty that there were deficiencies of the above minerals in the experimental animals.

<u>Summary of Blood Analyses</u>: The analyses of blood minerals and hematocrit before and after mineral supplementation in the final group of steers are summarized in Table 29. Although the lower and upper groups had significantly different serum iron concentrations at

the first sampling, this difference did not continue in the subsequent samplings. Concentrations of the minerals in blood declined after mineral supplementation. There were slight declines for calcium, sodium and potassium whereas notable reductions in serum iron, hemoglobin-bound iron and magnesium were noted.

Table 29

Summary of Blood Analyses of the Final Group of Steers (Lower and Upper Groups Combined) Before and After Mineral Supplementation

Blood Measurement	Mineral Supplementation		Percentage Change
	Before	After	
	Mean Concentration (ppm)		
Calcium	87.7	86.9	- 0.9
Magnesium	28.26	23.57	-16.6
Sodium	3807.4	3638.7	- 4.4
Potassium	383.4	377.7	- 1.5
Iron	13.82	9.84	-28.8
Hemoglobin-bound iron	348.0	282.7	-18.8
Hematocrit (%)	42.6	50.0	17.4

The relationship of calcium and magnesium is of interest in grazing cattle. Hypomagnesemic tetany (grass staggers) is associated with low serum magnesium and calcium. When these levels are sufficiently below normal, the animal's movements are stiff and staggering can occur, similar to the difficulty of movement observed in some of the steers in this experiment. Within a few hours or days of the initial signs, violent convulsions develop and death can occur rapidly unless the animal receives subcutaneous or intravenous injections of magnesium sulfate. Clinical signs can be observed when serum magnesium levels are 10-17 ppm (normal range is 19.4-26.7 ppm). Symptoms are certain to occur when concentrations of serum magnesium below 10 ppm are maintained. Almost all occurrences of the disorder are accompanied by a serum calcium concentration at or below 66 ppm (normal range is 90-120 ppm). The disease is often characterized by sudden and unexpected death.

There were gross signs that mild hypomagnesemic tetany may have occurred in the trial. Chronic hypomagnesemia is characterized by a stiff gait and a gradual loss of condition that can occur for several weeks without affecting appetite or body weight gain. This disturbance is often followed by spontaneous recovery or by the acute form of tetany. It is difficult to reconcile the blood levels of calcium and magnesium in this trial with even mild hypomagnesemic tetany based on a comparison of the "normal" levels of these minerals. However, it is possible that the metabolic requirement for calcium and magnesium may be elevated at high altitude. This would cause the observed levels to be low relative to the required concentrations, causing at least a mild hypomagnesemia detrimental to production.

The magnesium and calcium contents of the forage were only a fraction of those found in typical forage grasses. Because the dietary intake of these minerals was low, an extensive mobilization of calcium and magnesium from skeletal stores had to occur to maintain the blood concentration. Continued depletion and a low rate of mobilization of these minerals could retard growth over a long period of time.

Serum sodium concentrations remained slightly above to normal levels throughout the experiment. The pica, i.e. a craving for salt, observed during severe and prolonged salt restriction in cattle, was not observed in this trial. Other research at high altitude indicates that little change in serum sodium content occurs (140, 146, 269).

The serum potassium concentration of steers in this trial averaged approximately twice the normal level. Early studies indicated that either serum potassium levels were depressed (84) at altitude or there was no change (140). However, recent research has demonstrated that with a constant potassium intake at 14,100 feet of altitude, humans show a decline in urinary potassium and an increase in serum potassium (146). This is a net retention of potassium upon exposure to hypoxia and may be a protective mechanism beneficial to oxygen uptake, but it is counter-productive to the need for

increased urinary electrolyte excretion caused by the alkalosis produced by hypoxia. The excessive levels of potassium in the serum of the steers in this trial were a normal response to hypoxia but the concentrations were not high enough to reduce the growth rate.

The iron status of the blood in the steers of this experiment was unexpected. Mean serum iron concentrations were two to three times normal values. Hemoglobin-bound iron concentrations varied considerably, both greatly above and below normal levels. The mean concentration was below normal. This was unexpected because hemoglobin-bound iron is highly correlated with blood hemoglobin content which increases with altitude. Despite low total iron concentrations in the blood, the increased transport form of iron in the serum may have prevented severe iron deficiency anemia, permitting normal metabolism of the element by the tissues.

The continued increase of packed-cell volume in the blood during the trial was unexpected. An initial elevation of this blood component is expected in response to hypoxia, followed by a stable level sufficient to sustain the oxygen requirements of the steers. A long-term erythropoietic stimulus caused a steady increase in polycythemia. The initial response can be accounted for by the release of splenic reserves of red blood cells.

In summary, the serum mineral concentrations of calcium, magnesium, sodium, potassium and iron were not sufficiently different from normal values to have been major limiting factors to growth under the conditions of this trial. The low levels of iron in hemoglobin suggest that the hemoglobin content did not increase. Hemoglobin concentration per red blood cell may not have increased but, due to a considerable increase in the total number of red blood cells, total hemoglobin may have been elevated.

Forage Analysis

The native forage is the primary source of nutrients for livestock maintenance and production in the high altitude grasslands of Ecuador. The concentrations of organic and inorganic constituents of the forage are among the several determinants of the livestock production potential of the native forage in the area. Dry matter consumption, which is related to palatability of the forage, combined with the nutrient density and proportions of nutrients, can provide an estimate of the utility of the grasslands.

This trial was designed to estimate the nutrient yield of the *páramo* by measuring the growth of animals grazing the native herbage. The area was representative to the extent that the predominant forage of the site is *Stipa Ichu*. The nutrient yield could have been measured by periodically cutting and weighing small areas of the pasture and analyzing the forage. This method is imprecise for estimating potential animal production. It is difficult for the investigator to select a sample having a botanical composition and maturity equal to that consumed by grazing animals. The forage analyses of this trial provided additional information on the nutrient quality and quantity relative to typical forages used in low altitude dairy production systems. Although normal requirements of nutrients for high altitude production have not been established, the analyses provided a basis for comparative nutrition.

Proximate Analysis and Total Digestible Nutrients of Paja de Páramo: The proximate analysis and TDN of the principal forage in the *páramo* is shown in Table 30. Samples of young and mature *paja* were collected on four different dates. The dry matter content declined with maturity, but not significantly. The concentrations of crude protein and lipids (ether extract) increased as the plant matured. Concentrations of crude fiber and ash did not change significantly in the young plant, while the former declined with maturity and ash steadily increased. The changes in nitrogen-free extract (NFE)

Table 30

Proximate Analysis, Dry Matter Digestibility (DMD) and Total Digestible Nutrients (TDN) of Young and Mature _Paja de Páramo_ on a Dry Matter Basis

Sample Date	Dry Matter	Crude Protein	Crude Fiber	Ether Extract	Ash	NFE	TDN	DMD
	--------	--------	--------	Percentage	--------	--------	--------	--------
Young Paja:								
2/73	94.4	3.3	35.6	1.6	10.1	49.4	47.5	----
8/73	91.3	8.1	35.2	2.0	9.3	45.4	50.6	40.1
9/73	91.7	8.8	35.6	2.0	10.5	43.1	49.5	38.7
Mature Paja:								
6/73	94.0	5.3	38.6	1.7	10.5	43.9	47.1	32.1
8/73	92.4	6.0	36.6	1.7	10.4	45.3	48.1	31.9
9/73	90.9	6.8	35.1	2.6	11.9	43.6	48.2	35.8

reflected the changes in crude protein and ether extract. The high crude fiber content was at or above the highest crude fiber values observed in the better forages at their most mature stage, yet was slightly lower than the content of crude fiber in oat and wheat straws (199).

The total digestible nutrient content of the forage was similar at both stages of maturity and considerably below the values of higher quality grasses. Steers consuming normal amounts of dry matter generally need a diet containing about 50 percent TDN to meet their maintenance requirement. The steers in the experiment were able to meet their maintenance requirement and also gained body weight from forage containing less than 50 percent TDN. This suggests that the TDN requirement for growth was less at high altitude than at sea level. On the contrary, it is likely that the TDN requirement for energy was greater in the conditions of the experiment because of the almost daily rains and near-freezing temperatures during the night. If the maintenance requirement for TDN is, in fact, higher at altitude the steers must have consumed far greater quantities of forage than observed by similar cattle at low altitude grazing quality pastures. This does not seem likely because the condition of most of the steers was poor. They appeared thin until receiving the mineral supplement and spent much of the time lying down and grazing sporadically when they were standing up. Therefore, the dry matter intake must have been reduced below normal. The above observations indicate that the equations for calculating TDN may not include factors that are related to the high altitude conditions of this trial.

The crude protein content, even at the highest value of 8.8 percent, is at or below that of most grasses at the stage of greatest maturity when protein levels are low. Mean crude protein content is higher in the young than mature (paja de páramo), but the difference is not commensurate with the differences in stage of maturity between the samples.

The changes in nutrient content (Table 30) do not represent completely the true differences due to stage of maturity. The samples were taken randomly from several locations in the experimental site. Each composite sample was collected from similar locations on each sampling date, but no two serial samples were taken from the same plant. The stage of maturity was based more on the comparative stage of growth of young plants versus that of mature ones, and less on the stage of maturity related to initial stages of growth. Thus, the data provide some information on the nutritive value of the principal forage in the páramo, but are of little value for determining seasonal changes in nutrient composition.

Forage Digestibility: Table 30 includes the *in vitro* dry matter digestibility (DMD) of the *paja*, according to the method of Tilley and Terry (251). The mean DMD for young *paja* was 18 percent greater than mature *paja*, but the highest digestion coefficient of 40.1 was considerably below that of grasses commonly used in cattle production, such as mature bromegrass, ryegrass and bluegrass.

The *in vitro* organic matter digestibility (IVOMD) of *paja de páramo* is presented in Table 31. The value is the mean of four samples taken from the experimental site for the development of laboratory techniques which were included in the thesis research of another investigator in the Nutrition Laboratory (203). These data are presented for comparison and provide additional information on the chemical composition of the *paja de páramo* consumed by the steers in this trial. The organic matter digestibility of the forage was lower than the total dry matter digestibility. This, combined with a low organic matter content makes the forage a poor source of energy for rapid growth of cattle.

Cell-Wall Constituents and Ash, Silica and Nitrogen Content of Paja de Páramo: These analyses, obtained from research at INIAP (203) are presented in Table 31. The values for wheat straw are presented for

Table 31

In Vitro Organic Matter Digestibility, Cell-Wall Constituents, Silica, Ash and Nitrogen Content of *Paja de Páramo* and Wheat Straw

Analysis[b,c]	Chemical Composition as a Percentage of the Dry Matter[a]	
	Paja de Paramo	Wheat Straw
IVDMD	35.72 ± 3.73	----
IVOMD	29.88 ± 0.02	25.70 ± 0.77
NDF	72.14 ± 1.51	81.58 ± 1.43
ADF	47.70 ± 0.63	56.76 ± 0.69
ADL	6.97 ± 0.68	10.75 ± 0.73
Silica	9.11 ± 0.36	5.72 ± 0.05
Ash	10.50 ± 0.03	8.25 ± 0.03
Nitrogen	0.64 ± 0.02	0.71 ± 0.03

[a]All values are the mean of four samples except for IVDMD (five samples) ± standard deviation

[b]IVDMD = In vitro dry matter digestibility; IVOMD = in vitro organic matter digestibility; NDF = neutral detergent fiber; ADF = acid detergent fiber; ADL = acid detergent lignin

[c]All values derived from reference (203) except for IVDMD

purposes of comparison. Wheat straw is generally considered a poor source of nutrients for animal production and is marginally able to satisfy maintenance requirements.

The data in Table 31 include the percentage of the indigestible dry matter that is accounted for as total fiber (neutral-detergent fiber), lignocellulose (acid-detergent fiber), lignin (acid-detergent lignin), silica (a residue in ADF) and total ash, of which the major mineral in most grasses is silica. The data illustrate that *paja de páramo* is similar to wheat straw in its fiber fractions, is superior in organic matter digestibility and inferior in nitrogen content. The latter measurement, extrapolated by using a factor of 16 percent nitrogen in crude protein, estimates that *paja de páramo* contains 4.0 percent crude protein, whereas the level in wheat straw is 4.4 percent.

A silica content of greater than 2 percent depresses digestibility at the rate of three percentage units of digestibility for each increase of one percentage unit of silica (4). Thus, the *paja de páramo*, containing about seven percentage units of silica above the threshold, has a reduced digestibility of about 21 percent compared with a similar forage with less than 2 percent silica.

These data illustrate that the principal forage consumed in this trial was of poor quality and that the productive potential of the páramo in its natural state is limited, in part, by the scarcity of high quality forage.

Mineral Content of Paja de Páramo: Table 32 presents the mineral content of two composite samples of young paja and one composite sample of mature paja. Both the calcium and phosphorus content was significantly lower than that of many of the common forages such as ryegrass, bluegrass and bromegrass. The concentration of potassium in paja was only 5 to 10 percent of that measured in the common grasses. The level of sodium was comparable to that in forage legumes and grasses. The magnesium content ranged from one-tenth to one-fourth of the concentration measured in most forage grasses. The cobalt concentration was more than twenty-five times greater than the levels in legumes and cereal grains, which are usually higher in cobalt than are grasses. There is a wide range of normal manganese contents in most forages which is higher in forages growing in an acid soil such as that of the páramo. The manganese content of paja was in the upper half of the normal range. The copper content was approximately one-half the value of most forages. Zinc was present in paja at concentrations similar to legumes, which are usually

Table 32

Mineral Content of *Paja de Páramo* on a Dry Matter Basis

Mineral	Units	2/73 (young)	9/73 (young)	9/73 (mature)
Calcium	%	0.13	---	---
Phosphorus	%	0.04	---	---
Magnesium	%	0.04	0.047	0.056
Sodium	%	0.09	0.141	0.209
Potassium	%	0.21	0.282	0.314
Copper	ppm	6.0	---	---
Cobalt	ppm	4.0	< 4.0	< 4.0
Manganese	ppm	5.0	435.0	302.0
Selenium	ppm	--	< 100.0	< 100.0
Arsenic	ppm	--	< 40.0	< 40.0
Molybdenum	ppm	--	< 40.0	< 40.0
Zinc	ppm	--	4.0	19.0
Chromium	ppm	--	< 4.0	< 4.0

much higher than forage grasses. The minimum detectable levels of selenium, molybdenum, chromium and arsenic were above the normal levels measured in plants. Therefore, the presence of deficient or toxic concentrations of these micronutrients could not be established.

Summary of Forage Analyses: The principal forage consumed by the steers in this trial was low in protein, TDN, fat and digestibility and had high contents of fiber and ash compared to the common forage grasses. The protein and TDN levels were apparently not low enough to prevent body weight gain. Also, they were not sufficiently high to permit the higher rates of gain possible in steers consuming good quality forage. The steers could gain body weight under the nutritional and environmental stresses of the experiment. This suggests that the forage is not devoid of nutritional merit and can make some contribution to the energy needs of cattle grazing solely on *paja de páramo*. The ability to utilize forage at high altitude is species-dependent. For example, the ability of the alpaca to digest the protein, fat and fiber of forage is much greater than for sheep (9). The TDN of the same feed at high altitude is 15 to 30 percent higher in the alpaca than in the sheep. The ability of the bovine to convert poor quality roughages to meat at high altitude may be limited.

There were severe deficiencies in the forage of calcium, phosphorus, magnesium and potassium. There was only one-half the normal level of copper. Excesses were noted for sodium, cobalt and zinc. Although the analysis was imprecise, there may have been some selenium toxicity, but this was not observed during the trial.

Just as urea may have been beneficial to growth rate, a mineral mixture, balanced to provide the mineral requirements of the steers, should enable efficient metabolism and utilization of the forage consumed. Even the highest quality forage can be inefficiently utilized if the mineral status of the animal is unbalanced.

Soil Analyses

The mineral content and pH of two composite samples of the lower and upper pastures are presented in Table 33. The interpretation of the mineral status of the soils was made by the Soils Laboratory of INIAP. Potassium, copper and zinc were present in normal amounts in both soils. Nitrogen was high in the lower soil and normal in the upper pasture. Both soils had excessive levels of calcium, magnesium and iron. There were deficiencies of phosphorus and manganese in the soil. The pH was slightly acidic but within the normal range.

Table 33

Soil Mineral Content and pH of the *Páramo* Pastures

Soil Measurement	Lower Pasture	Upper Pasture
Calcium (ppm)	600	625
Iron (ppm)	126	108
Potassium (ppm)	105	105
Magnesium (ppm)	100	105
Phosphorus (ppm)	8	10
Nitrogen (ppm)	68.0	55.0
Manganese (ppm)	12.0	13.5
Zinc (ppm)	7.6	7.2
Copper (ppm)	4.0	3.2
pH	5.6	5.6

One difficulty encountered in the interpretation of soil mineral data in Ecuador is the relationship of local concentrations to established "normal" values. The soil chemists there have monitored the soils of the *sierra* for several years and have determined the contents of soil minerals in many areas. But the interpretation of whether the concentration of a particular mineral is low, medium or high is based on data of soil, plant and animals established elsewhere, few of which are derived from areas having soil of volcanic origin. INIAP has only recently begun studies to determine "norms" of mineral requirements of native species of plants and animals, of soil fixation, the effect of organic matter content and the ratios of inorganic to organic phosphorus. As norms are established for the local conditions interpretations of mineral status will become increasingly relevant. For example, although phosphorus concentration in volcanic soils is low, if its availability in the soils of Ecuador is greater than elsewhere, the soil content could remain below that of established norms yet be sufficient for plant and animal production. Much more research is needed to define more precisely the nutrient status of soils, plants, animals and humans.

A good example of the "state of the art" of interpretation of mineral status in Ecuador is the role of magnesium in the soil-plant-animal relationship. The analysis of soil magnesium led to the interpretation that it was present at a high level. But this level did not produce excessive plant uptake, because the magnesium in the forage was only a small fraction of that found in most forage grasses utilized at low altitude. The extremely "low" plant magnesium level should have led to severe deficiency of this element in the animal consuming paja de páramo. On the contrary, the serum magnesium concentrations were in the upper portion of the normal range. The requirement for magnesium may be lower at high altitude, but this remains to be determined. Perhaps the availability of magnesium in the plant is considerably greater under the conditions of the experiment, to an extent that provides adequate utilization of the mineral. Also the magnesium may be in forms more readily absorbed by the gastrointestinal tract of the animal. The steers probably consumed magnesium in enough soil and water to maintain adequate levels of the element in the serum.

The soil pH of 5.6 lies in a normal range of pH 5.5-6.5. The availability and solubility of soil minerals such as calcium, phosphorus, magnesium, manganese, zinc, iron, cobalt and boron are greatest in organic soils having a pH of 5.0-6.0. Below pH 7.0 the availability of molybdenum is low especially in organic soils. Most soil minerals in this trial should have been highly available for incorporation into the *paja de páramo*, although some were present in low quantities in the soil.

Mineral Interrelationships

The mineral interrelationships of most interest in this trial may include calcium-phosphorus-magnesium, copper-molybdenum-sulfate and magnesium-potassium. The availability of calcium and phosphorus in the soil has long been known to be interrelated. These minerals are also interrelated in uptake by the plant and in the nutrition of the animal. In this experiment the high calcium level in the soil was not reflected in the

plant content, yet the steers were only mildly hypocalcemic. The low accumulation of calcium in the plant may reflect of low soil phosphorus. The moderate hypocalcemia was a result of depressed intake of forage as well as its low calcium content. High soil magnesium can depress calcium incorporation by the plant. Low plant and blood phosphorus combined with relatively high calcium intake can reduce cellulolytic digestion in the rumen. The normal magnesium, low calcium and possibly low phosphorus in blood may have played a major role in the skeletal deterioration noted in the steers after several months of grazing a forage having low levels of all three minerals. A depressed intake of forage low in phosphorus could have aggravated the nutritional stress. A high phosphorus diet normally increases the magnesium requirement. Because the intake of phosphorus was low the magnesium requirement probably was not elevated.

A prolonged intake of forage having low calcium and magnesium content could lead to hypomagnesemic tetany. If this state developed at all in the trial, it was neither debilitating nor was a cause of death.

The copper-molybdenum-sulfate interaction can only be speculated upon in this trial because the levels of these minerals in blood were not determined. Molybdenum and sulfate can prevent the toxicity of copper by reducing its concentration. The binding of copper by molybdenum compounds and sulfate in the soil and plant also makes copper less available to plants and animals, especially the ruminant. The results of unpublished experiments at INIAP suggest that soil and plant sulfur may be low. This, combined with the lack of diagnosable copper deficiency or toxicity in the present experiment, suggests that the nature of the relationship of these three minerals was not a deleterious factor for the growth and survival of steers in the *páramo*.

Magnesium and potassium are interrelated both in soil and in animals. A magnesium deficiency can occur in soils having high levels of potassium that interfere with magnesium uptake by plants. The data indicate that this was not a factor in the trial. A high intake of potassium by animals can decrease magnesium absorption. This also did not occur in the trial, because potassium intake was low and magnesium blood levels were in the normal range. The high potassium content in the blood apparently had no deleterious effect on magnesium concentration in the blood. The opposite situation, low potassium and above-normal magnesium in soils and animals, usually does not interfere with normal plant uptake or animal metabolism.

Mineral Supplementation

Supplementing the diet of the steers with a mineral mixture balanced to meet the requirements for normal growth at low altitude resulted in dramatic increases in the rate of daily body weight gain, despite a decline in serum mineral concentration. The decline may have been caused by increased tissue storage and/or utilization of the minerals. It is possible that increased excretion occurred due to alkalosis produced by hypoxia. On the other hand, depletion of body stores of some minerals may have occurred prior to mineral supplementation. The additional mineral intake may have prevented a severe depression of serum mineral content toward the end of the experiment.

The inclusion of urea in the mineral supplement may have been a significant factor in the dramatic increase in rate of gain. The steers were consuming a nitrogen-poor forage in which the ratio of protein to calories was wider than required for normal productive performance. The mean crude protein in the forage was 6.4 percent. Based on a mean body weight of 300 kg just prior to mineral supplementation, a normal dry matter intake of 2.9 percent of body weight per day leads to a consumption of 8.7 kg of forage dry matter or 557 grams of crude protein. The daily crude protein requirement is 745 grams for a 300 kg steer gaining 1 kg of body weight per day.

Thus, there was a deficit of 188 gm of crude protein per day for normal average daily body weight gain. The mineral mixture contained 12.8 percent of urea. The mean daily consumption of the mixture was 340 gm per steer, providing an average of 43.5 gm urea daily to each animal. Using a protein-equivalent value for urea of 2.62, the intake of the mixture would raise the protein-equivalent daily intake by 114 grams. The total intake of crude protein, or its equivalent, from forage and urea should be sufficient to meet the requirements for a daily gain of 500 gm under normal circumstances. The maintenance requirements of all nutrients are unknown for high altitude conditions. It was estimated that dry matter intake by the steers was reduced to one-half the normal level. Even so, the urea content of the diet did not exceed 1 percent of the dry matter, above which urea toxicity may occur. Because the amount of urea provided by the supplement accounted for a large portion of the protein requirement, it is clear that urea played a major role in the increase of body weight gains.

Molasses was added to the ration to improve palatability and assure the desired intake of the mixture. The molasses contributed about 2.6 percent of the megacalories of net energy required for maintenance and an ADG of 1.0 kg for a 300 kg growing steer. Therefore, the molasses played only a small role in the changes of body weight that occurred after mineral supplementation began.

Based on the results of this study, male Holsteins not only can satisfy their maintenance requirements, but can achieve a moderate rate of gain with the native forage as the sole source of nutrients. Ad libitum feeding of a mineral mixture, containing urea and balanced to correct deficiencies in the herbage, doubled the rate of body weight gain of steers. Although this is a major metabolic response, given the conditions of the experiment, the average daily body weight gains were low compared with those obtained in feedlot conditions at low altitude. This low metabolic efficiency in the páramo should be profitable, however, because of inexpensive labor, land and feed costs. Once the experimental site had been established the daily direct input costs of labor and minerals were (U.S. dollar equivalent) five cents and 3.5 cents per animal. The return from daily liveweight gain (based on an ADG of 212.5 gm in the final group of steers during mineral supplementation) was eleven cents, yielding a gross income over labor and feed costs of 2.5 cents daily per steer. Direct labor costs are essentially fixed within limits, i.e., one herdsman is required full-time regardless of herd size up to a limit which was not approached in this study. Up to this limit direct labor costs decrease per animal as the herd size expands. Land costs have the same characteristic for small herds as do fencing and roads. Total costs of the supplement are essentially variable because they vary with the number of cattle being fed. The mineral cost per animal is related to body size because consumption depends on this variable.

Observation of the Steers

Several observations noted during the trial were difficult to quantify, yet they may contribute to an understanding of the nature and stress of the experimental conditions.

During the month previous to being sent to the *páramo*, the original group of forty-eight steers and nine others were maintained in a pasture located just below the experimental site. This pasture ranged in altitude from 10,500 to 11,000 feet. All of the steers grazed normally, although the pasture was of only moderate quality. They showed normal vigor and few signs of stress. They were wary of humans but were not wild. Their hair appeared normal and showed no signs of mineral deficiency. Some of the younger steers became ill, however, and were not selected to be sent to the *páramo*.

Shortly after ascent to the páramo the steers became lethargic and the hair became rough on several animals. Many of the steers would lie down for long periods instead of grazing frequently. Most animals would rise when approached by humans but would make little effort to maintain a distance greater than ten feet. It was necessary for the herdsman to move continually between groups to encourage the animals to graze the entire pasture at each altitude. The steers became less wary as the altitude increased, behaving as if in a stupor.

As the trial progressed some physical deterioration became noticeable and the lethargy of the steers stabilized. Most steers were thin prior to mineral supplementation. After consuming minerals they filled out and appeared healthier and less lethargic. The most prominent change in many steers was a pronounced "winging" of the shoulders. This was accompanied by drooping heads and sagging backs. At times some steers showed an unnatural gait when walking or running, which is best characterized as staggering. The lack of coordination was also evident when rising to graze was accomplished with difficulty. The staggering and difficult coordination appeared sporadically for a few days and then disappeared. Some previously affected animals never displayed these signs later in the trial, while others did. The degree and types of symptoms were highly variable with no apparent relationship to size, season or other experimental variables.

The loss of steers over the cliff and in the ditch suggested that vitamin A deficiency possibly was causing night-blindness. All steers were treated with injectable vitamin A at 280 days of the experiment. Only one steer died from physical causes after this time. Fence construction was probably the major factor that reduced the number of deaths due to falling.

The behavior of four animals in the upper group, consisting of one bull and three steers, was notably different from that of the others. All four animals survived the trial. After only a few weeks of residence in the páramo, they continually grazed in the upper half of the high altitude pasture and descended only for water and minerals. They were among the most vigorous animals of the trial and preferred to graze at an altitude at least 500 feet higher than the rest of the group. They often ascended to the upper limits of the pasture during the day. Their initial mean body weight was 294 kg, their final mean body weight was 328 kg. The ADG of these steers for the trial was 89 gm. A considerable amount of energy probably was expended during extensive grazing, which could account for their ADG being below the mean for the group. Their propensity

for grazing at high altitude may have a genetic basis, which is related to the ability to withstand the nutritional and environmental rigors of high altitude. This would permit the selection and breeding of cattle for maximum production at high altitude, which could substantially reduce mortality and permit higher rates of gain under these conditions.

CHAPTER V

CONCLUSION AND RECOMMENDATIONS

The government of Ecuador was interested in conducting research to determine if high altitude grasslands could be used as a resource for livestock production. Utilization of this area could expand the nutrient resource base of the country for meat and wool production. Thousands of newborn dairy males that could be raised in the _páramo_ are presently slaughtered each year because the lack of perceived production alternatives. Vast areas of grasslands at high altitude are presently unused or under-utilized. Credit is available to support substantial expansion of agricultural production in the country.

Conclusion

The results of this experiment demonstrate conclusively that Holstein cattle can grow in the _páramo_ consuming only native forage and water. Appropriate nutrient supplements can enhance appreciably the growth of livestock grazing at high altitude. Disease control

and appropriate fence construction must be employed to reduce livestock mortality. Nutrient deficiencies affect livestock production at high altitude greater than does the reduced partial pressure of oxygen.

Recommendations

There is a need for additional research in the soil-plant-animal-human relationship to provide a basis for the economic development of the *páramo* for livestock production. These relationships are of most practical significance if improvement of the human diet is the ultimate target of changes in agricultural production. The primary research necessity is to investigate thoroughly three nutritional aspects of livestock production at high altitude: (1) the metabolism of macro-elements and micro-elements; (2) nitrogen metabolism; and (3) the nutrition of young animals. Implicit in all research is exhaustive economic analysis of each experiment to determine the course of subsequent research and implementation of production practices.

The mineral requirements for high altitude livestock production must be established. This information will contribute to the knowledge of agricultural production at lower altitude in the *sierra*. This research will result in the formulation of appropriate mineral supplements and fertilizers for high altitude conditions.

Investigations of nitrogen metabolism should examine nonprotein nitrogen as a nutrient, as well as protein and its constituent amino acids. Nitrogen and mineral supplementation are metabolically interdependent and, when dietarily balanced, can improve the efficiency of total nutrient utilization.

Investigations of calf nutrition from birth to six months of age should be emphasized. The younger steers in the *páramo* trial were unable to withstand the nutritional and environmental stress. Proper calf nutrition can provide healthy animals that will survive the transitions from lower to higher altitudes and from high quality pastures to the low quality forage of the *páramo*.

A second major area of research in the *páramo* should focus on improvement of the forage. Fertilization studies and the introduction of legumes and grasses should be continued. Subsequent research should examine management of forage using pasture rotational systems with different animal densities. These agronomic studies can improve utilization of the available land for nutrient production.

Nutritional studies and research on pasture improvement will provide a basis for investigating livestock production options in the *páramo*. These options include the use of a combination of steers and sheep, or cow-calf operations utilizing beef cattle breeds suited for high altitude conditions. A system of gradual transition of animals to high altitude should be considered. In addition, livestock could be sent to feeding centers for finishing prior to marketing. Steers should be marketed at weights below current standards to take advantage of the feed efficiency of the young animal.

Large quantities of animals, homogeneous with respect to age, body size and breed, should be used to assess livestock responses. A wide range of ages and body sizes make it difficult to isolate the response of livestock to other experimental variables. These variables should include:

A. Altitude--the cold, wet and windy conditions of altitude probably affect livestock performance more than a low partial pressure of oxygen. Shelters from wind and rain may be of benefit in the *páramo*. Because of the relatively narrow range of altitudes in the *páramo*, differences of altitude within this area need not be a major variable.

B. Location--the climatic and physiographic diversity of the *sierra* is sufficiently great to require that similar research should be conducted in several high altitude locations.

The suitability of other areas of _páramo_ for livestock production must be established. More information is needed before recommendations can be made for widespread utilization of these grasslands.

A summary of the priority research needs for development of the _páramo_ is outlined below:

A. General Statement

1. In all studies, the confounding effects of altitude, species of livestock and species of forage must be isolated. For example, to study the effect of altitude the type of animal and variety of forage must remain constant.
2. Economic analysis of all experiments is essential both for subsequent research and for adoption of production practices.
3. Permanent meteorological stations should be established in the _páramo_.

B. Nutritional Research

1. The determination of the mineral requirements and appropriate supplements for livestock in the _páramo_ is of highest priority. Even the best of feeds are inefficiently used without a mineral supplement balanced to meet metabolic requirements.

2. The interrelationships of minerals in the soil-plant-animal-human sequence must be determined to understand the point at which mineral application is best utilized. For example, nitrogen may be applied to the soil to produce more forage, or nitrogen could be fed directly to the animal. Either one option, or the combination of two options, will provide the best utilization of scarce nitrogen resources.

C. Pasture Improvement

1. Fertilization of the soils in the _páramo_ should focus primarily on increasing the growth of the native forage.
2. Pasture rotation can improve the harvest of the plant nutrients by livestock. Studies of animal density combined with pasture rotation will determine the appropriate stocking rate to best utilize the seasonal nutrient production of the _páramo_.
3. Legumes and grasses adapted to high altitude must be studied under the conditions of the _páramo_. The establishment of forages higher in nutritional quality can reduce the need for costly dietary supplements.

D. Production Alternatives

1. It is essential that the nutrient production of the *páramo* be efficiently harvested. The following production systems should be investigated:

   a. Grazing of dairy steers, beef steers or sheep;

   b. A combination of cattle and sheep;

   c. Cow-calf operations using beef cattle.

2. The above production alternatives should include a system of fattening the offtake animals at lower altitudes prior to marketing.

E. Studies must be conducted on the adaptation of livestock species to the stress of high altitude conditions in the *páramo*. There are significant differences in adaptive ability both within and among animal species.

F. Thorough investigation of the etiology and control of disease is apparent from this study. The prevalence in Ecuador of most animal diseases is a limiting factor to improvements in livestock production.

APPENDIX

APPENDIX

Table 34

Individual Body Weights of the Lower Group of Steers on Each Weighing Date[a]

An. No.	Feb 20	Feb 21	Feb 22	Jul 9	Jul 10	Jul 11	Oct 15	Oct 17	Oct 18	Nov 28	Jan 17	Mar 11	Mar 12	Mar 13
3	193	187	187	---	---	---	---	---	---	---	---	---	---	---
4	403	408	410	405	404	407	434	453	454	446	476	495	489	484
7	354	331	335	331	331	337	379	388	378	401	413	434	429	427
8	383	363	371	367	364	373	406	420	413	440	460	479	470	470
9	337	310	331	317	302	315	307	318	316	316	319	315	315	314
10	217	208	221	236	228	236	257	254	256	241	260	260	253	261
11	338	337	340	321	322	326	322	340	337	329	332	338	346	334
18	294	293	294	293	295	303	307	320	306	286	286	292	300	302
20	159	152	155	153	152	156	158	159	158	159	157	---	---	---
22	202	188	193	195	191	197	208	205	204	196	215	228	220	228
25	192	183	191	186	185	192	213	214	210	209	220	221	223	218
27	167	162	162	174	174	179	184	197	188	210	239	233	240	245
29	184	178	180	193	186	196	196	206	196	207	226	221	231	223
30	258	240	257	267	273	270	316	320	326	328	364	381	375	365
31	135	127	127	137	136	142	---	---	---	---	---	---	---	---
33	127	120	128	---	---	---	---	---	---	---	---	---	---	---
34	146	147	151	117	119	118	140	140	139	136	136	---	---	---
37	142	131	134	122	128	126	---	---	---	---	---	---	---	---
40	396	380	388	350	350	351	366	378	379	375	352	354	370	357
41	346	319	329	332	326	336	351	360	347	335	330	331	329	323
42	428	431	419	454	454	455	483	506	498	516	560	564	551	544
45	227	224	225	---	---	---	---	---	---	---	---	---	---	---
46	300	295	311	302	296	302	323	333	332	327	324	321	323	321
47	294	277	279	291	295	305	306	307	302	308	308	328	330	330

[a]All values are Kilograms.

Table 35

Individual Body Weights of the Upper Group of Steers on Each Weighing Date[a]

An. No.	Feb 20	Feb 21	Feb 22	Jul 9	Jul 10	Jul 11	Oct 15	Oct 17	Oct 18	Nov 28	Jan 17	Mar 11	Mar 12	Mar 13
1	276	268	265	274	272	282	288	293	288	290	310	329	327	325
2	302	286	283	299	298	303	305	295	298	298	314	317	316	312
5	400	391	388	381	381	381	390	383	383	381	407	398	386	384
6	397	378	373	373	374	385	409	409	403	414	443	447	445	441
12	191	191	196	214	214	219	217	223	221	214	227	226	238	235
13	332	324	333	325	327	339	350	354	341	350	361	380	375	371
14	248	229	237	236	239	240	---	---	---	---	---	---	---	---
15	229	216	222	---	---	---	---	---	---	---	---	---	---	---
16	326	308	327	348	342	344	336	344	339	330	350	369	359	360
17	302	289	309	296	289	299	283	284	280	278	302	311	310	295
19	425	422	418	405	402	410	463	476	467	484	512	535	520	522
21	171	163	168	170	170	172	---	---	---	---	---	---	---	---
23	144	145	144	145	146	150	141	142	152	152	---	---	---	---
24	162	153	156	158	162	164	145	142	144	---	---	---	---	---
26	208	198	204	213	214	217	219	212	215	228	243	254	244	250
28	189	187	178	178	176	177	---	---	---	---	---	---	---	---
32	341	343	338	---	---	---	---	---	---	---	---	---	---	---
35	132	128	126	---	---	---	---	---	---	---	---	---	---	---
36	153	146	142	143	144	146	143	144	147	152	---	---	---	---
38	133	129	133	140	143	144	---	---	---	---	---	---	---	---
39	169	171	172	---	---	---	---	---	---	---	---	---	---	---
43	438	418	423	424	411	432	413	436	410	422	---	---	---	---
44	179	185	182	185	188	197	189	199	190	186	207	244	244	246
48	364	364	368	397	393	399	376	377	376	382	386	399	387	406

[a]All values are Kilograms.

Table 36

Concentrations of Calcium, Magnesium, Sodium and Potassium in the Serum of Steers in the Lower Group on Each Sampling Date

An. No.	Serum Calcium			Serum Magnesium			Serum Sodium			Serum Potassium		
	7/10	10/17	3/12	7/10	10/17	3/12	7/10	10/17	3/12	7/10	10/17	3/12
	ppm											
4	79.0	79.0	81.0	28.19	24.19	26.91	3153.7	3948.6	3595.6	351.1	395.8	416.7
7	80.3	83.1	59.9	26.77	29.01	18.21	3128.1	3552.2	2702.5	367.9	369.4	363.2
8	94.1	88.1	88.1	30.11	30.63	26.99	3179.3	3538.2	3842.2	408.5	429.6	464.5
9	98.8	85.2	92.3	31.69	28.03	22.42	3496.3	3442.2	3812.2	355.8	352.6	327.4
10	95.1	96.2	77.4	29.26	27.80	18.26	3428.4	3918.3	3128.1	364.9	374.0	317.1
11	88.1	73.5	69.9	26.09	22.41	19.87	3256.7	3709.8	3078.4	311.2	372.6	301.4
18	87.6	98.8	91.6	27.24	36.26	23.45	4202.1	4089.4	3524.2	446.0	538.2	410.2
20	66.2	77.2	--	23.22	23.98	---	4202.1	3103.8	----	413.4	397.6	---
22	92.1	70.9	86.2	26.39	23.22	22.30	4153.7	3456.1	3538.2	281.3	310.0	351.1
25	92.3	103.2	91.8	29.01	30.02	23.64	3694.2	4419.9	4121.5	294.0	311.2	302.6
27	76.3	86.2	85.7	26.70	22.21	25.40	3608.2	4010.8	3948.6	340.7	328.9	358.7
29	83.1	72.0	80.8	25.05	24.84	23.32	4506.8	3753.8	4089.4	349.6	351.1	361.7
30	110.9	112.4	93.6	33.27	33.27	27.80	4301.0	3768.0	4089.4	426.4	464.5	490.2
31	99.6	---	--	29.60	---	---	4524.8	----	----	426.4	---	---
34	79.4	80.8	--	21.61	23.56	---	3964.5	3724.0	----	323.0	342.2	---
37	94.6	---	--	27.80	---	---	4268.5	----	----	408.5	---	---
40	103.7	95.9	98.8	26.93	27.08	21.99	4121.5	3388.3	3709.8	331.9	345.2	361.7
41	85.7	87.6	82.0	26.93	29.51	17.27	3782.3	3680.1	3469.9	364.9	371.1	363.2
42	95.7	89.1	103.4	26.63	28.84	26.40	5346.9	3580.2	4010.8	415.1	405.5	403.8
46	79.2	74.8	90.8	26.54	29.85	24.10	4301.0	3320.9	3812.2	484.9	531.0	410.2
47	74.1	74.3	87.4	23.91	26.31	21.08	3665.9	3388.3	3442.2	391.1	439.5	397.6

Table 37

Concentrations of Calcium, Magnesium, Sodium and Potassium in the Serum of Steers in the Upper Group on Each Sampling Date

An. No.	Serum Calcium			Serum Magnesium			Serum Sodium			Serum Potassium		
	7/10	10/17	3/12	7/10	10/17	3/12	7/10	10/17	3/12	7/10	10/17	3/12
1	78.5	65.4	78.3	28.44	27.71	22.74	3902.5	3595.6	3980.4	371.1	369.4	340.7
2	106.2	96.2	71.6	33.75	32.52	20.85	3827.9	4284.7	3388.3	467.9	479.9	500.7
5	83.6	89.8	68.4	29.01	29.60	22.55	3334.7	3666.0	3552.5	389.6	431.3	372.6
6	79.0	64.8	96.7	28.19	23.77	24.78	2793.1	3709.8	3666.0	457.7	498.9	516.7
12	70.5	94.4	88.1	23.01	27.63	21.20	4268.5	4318.8	3738.2	295.5	305.6	312.7
13	85.7	87.1	106.0	29.43	31.07	28.67	4595.6	3768.0	3753.8	342.2	314.2	387.9
14	65.6	--	---	24.91	---	---	4057.3	----	----	441.0	---	---
16	86.7	89.1	78.8	25.79	30.28	21.93	3496.3	3229.5	3622.3	367.9	399.1	339.2
17	92.8	90.8	89.3	32.89	33.56	27.82	4630.4	3666.0	3858.0	367.9	339.2	328.9
19	96.4	103.7	108.8	30.98	30.19	28.35	4776.4	3191.5	3483.8	345.2	366.4	367.9
21	67.0	--	---	27.32	---	---	3932.8	----	----	413.4	---	---
23	99.1	72.6	---	27.63	25.27	---	3724.0	3140.9	----	343.7	403.8	---
24	70.3	81.7	---	27.16	27.87	---	3738.2	3442.2	----	371.1	361.7	---
26	95.9	90.8	105.7	26.31	24.54	25.40	3994.9	3552.2	3827.9	312.7	304.1	304.1
28	81.5	--	---	26.16	---	---	3608.2	----	----	400.8	---	---
36	87.6	71.3	---	28.93	22.01	---	3964.5	2712.8	----	413.4	304.1	---
38	85.5	--	---	28.12	---	---	3469.9	----	----	328.9	---	---
43	81.5	80.6	---	26.54	28.27	---	3538.2	3388.3	----	384.9	386.4	---
44	90.8	90.8	82.6	24.54	31.07	22.93	3308.6	3622.3	3334.7	432.8	476.4	491.9
48	67.6	100.4	86.4	25.34	35.54	26.84	4946.9	4057.3	3402.1	410.2	418.2	289.9

Table 38

Concentrations of Serum Iron and Hemoglobin-bound Iron and Percentage Packed-Cell Volume in the Blood of Steers in the Lower Group on Each Sampling Date

An. No.	Serum Iron			Hemoglobin-bound Iron			Packed-Cell Volume		
	7/10	10/17	3/12	7/10	10/17	3/12	7/10	10/17	3/12
4	15.26	16.26	13.07	462.3	552.2	356.7	39.4	43.9	53.7
7	10.25	17.09	10.53	583.7	337.7	210.9	43.6	43.4	48.0
8	9.23	15.31	8.12	448.0	242.1	384.8	41.6	47.5	68.4
9	8.45	16.35	7.13	107.4	340.9	181.5	37.6	38.6	36.0
10	9.19	9.19	9.23	276.6	178.4	290.7	36.7	40.2	51.5
11	8.56	21.10	7.98	489.8	553.5	264.9	32.7	47.0	55.6
18	10.06	14.53	8.27	174.7	281.3	147.4	41.6	40.6	47.5
20	8.02	13.95	--	439.7	243.6	--	39.2	40.4	--
22	21.91	18.78	8.82	603.7	521.6	312.8	44.7	48.4	48.0
25	10.76	9.87	10.97	314.9	154.7	274.0	44.1	46.0	45.2
27	11.33	13.86	13.07	489.8	392.6	360.9	46.8	45.9	48.5
29	22.69	17.29	10.45	492.4	462.3	369.7	42.7	47.6	52.0
30	13.68	11.37	13.42	151.6	171.3	405.3	46.5	43.8	49.0
31	10.61	--	--	273.8	--	--	43.1	--	--
34	11.57	16.07	--	654.7	254.3	--	36.0	37.9	--
37	16.26	--	--	259.0	--	--	36.3	--	--
40	10.41	10.76	8.27	161.7	150.3	188.5	40.0	41.4	54.5
41	10.06	15.59	7.27	347.1	242.8	313.8	41.6	54.5	66.0
42	18.67	15.03	8.97	125.3	261.3	230.9	45.1	45.5	33.3
46	24.07	18.62	7.80	541.3	426.4	245.4	37.6	36.8	46.0
47	14.76	15.49	6.82	519.0	369.5	209.3	33.5	35.9	52.9

Table 39

Concentrations of Serum Iron and Hemoglobin-bound Iron and Percentage Packed-Cell Volume in the Blood of Steers in the Upper Group on Each Sampling Date

An. No.	Serum Iron			Hemoglobin-bound Iron			Packed-Cell Volume		
	7/10	10/17	3/12	7/10	10/17	3/12	7/10	10/17	3/12
1	12.19	18.73	8.45	542.4	491.1	385.8	41.4	43.8	62.4
2	8.34	12.23	11.81	122.2	348.1	371.5	42.2	43.1	49.5
5	10.18	16.40	12.06	436.8	285.0	399.6	43.0	42.0	59.6
6	9.84	18.99	10.33	526.5	578.2	172.9	41.7	54.7	62.6
12	10.76	16.30	12.69	432.9	234.3	348.1	38.6	42.5	44.1
13	10.41	9.84	7.66	350.0	116.7	150.3	37.0	38.8	38.0
14	13.20	--	--	492.4	--	--	40.0	--	--
16	12.60	15.26	9.79	526.0	289.6	328.6	41.0	53.3	59.6
17	10.25	12.23	11.86	415.0	186.2	308.9	40.2	41.7	42.0
19	8.45	12.90	10.25	441.0	172.1	166.1	39.2	42.7	46.5
21	21.27	--	--	617.0	--	--	36.3	--	--
23	6.51	17.14	--	109.7	354.4	--	45.1	45.2	--
24	8.86	14.22	--	413.4	253.2	--	39.0	41.2	--
26	9.08	15.64	8.49	357.2	205.1	99.8	40.0	45.8	43.8
28	9.26	--	--	407.7	--	--	38.0	--	--
36	14.58	9.60	--	642.5	236.9	--	45.9	48.5	--
38	8.93	--	--	556.9	--	--	37.0	--	--
43	13.03	18.88	--	464.9	411.1	--	47.1	50.0	--
44	12.86	13.81	14.98	492.4	217.4	404.0	38.0	41.8	41.0
48	6.21	9.56	6.82	318.5	169.0	314.9	49.5	48.5	44.6

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