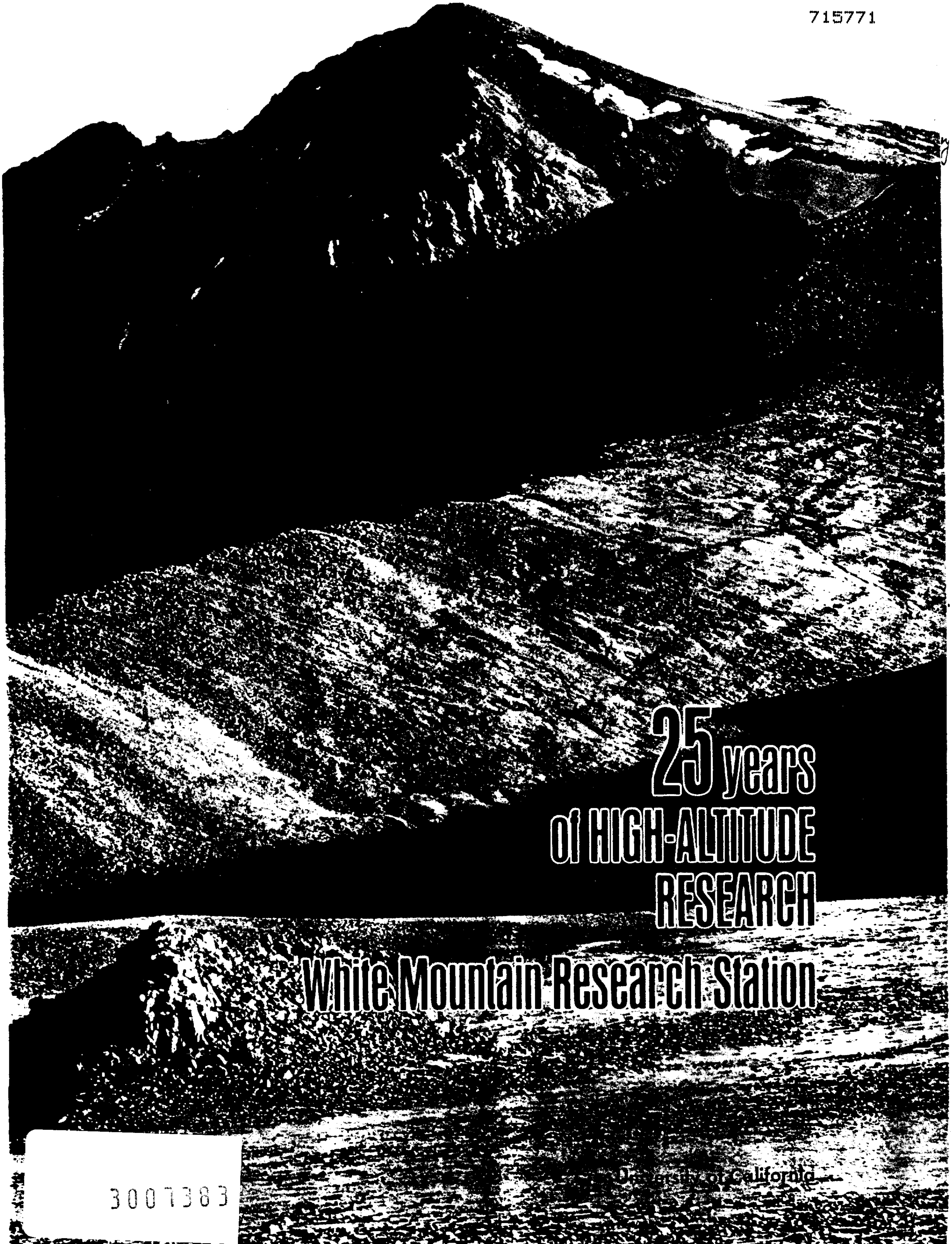
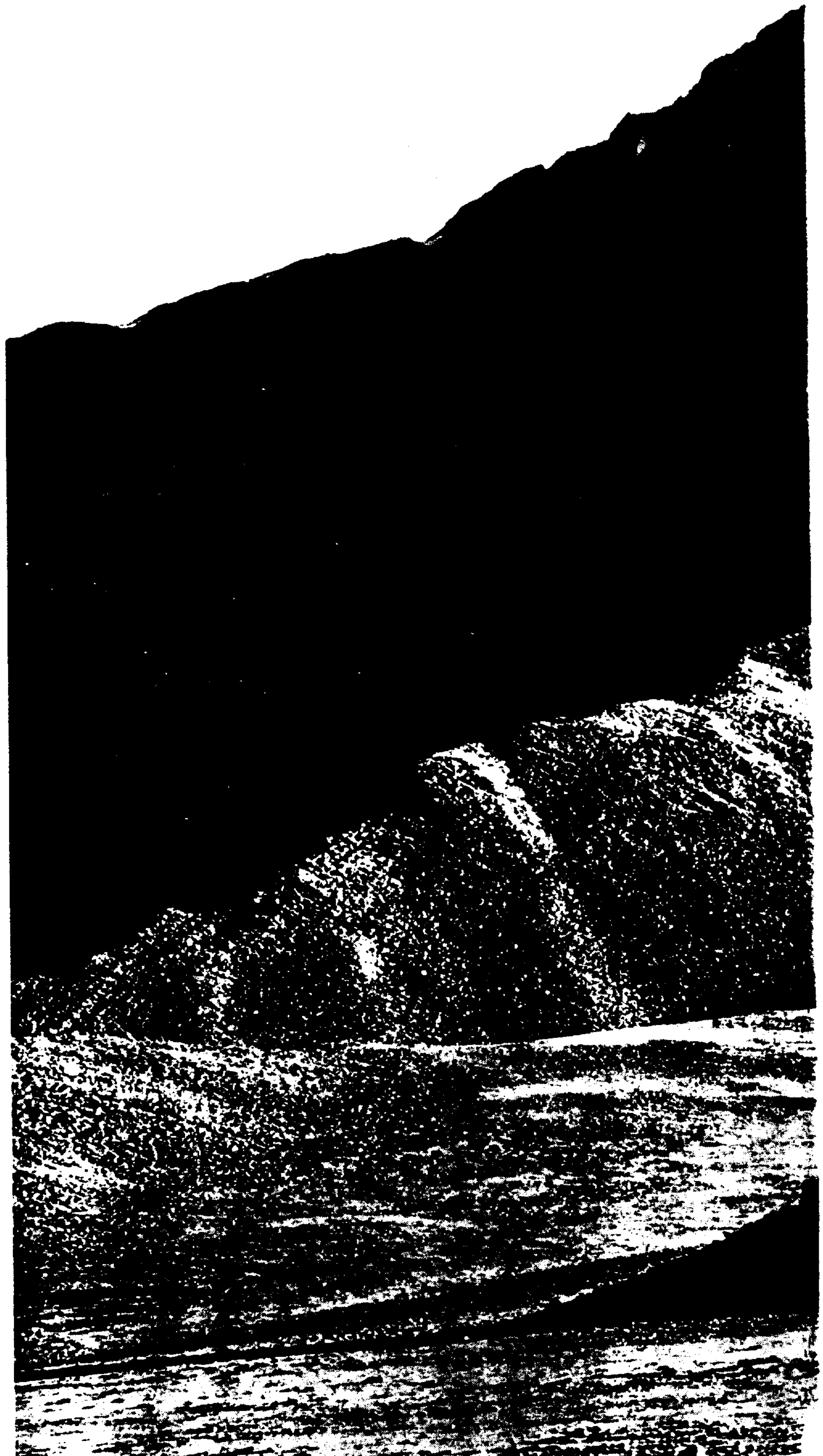

25 years
of HIGH-ALTITUDE
RESEARCH
White Mountain Research Station
University of California



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27. Inge, W.H., Jr.
Physiology. University of California, Berkeley, June 1972.
Effects of hypoxia on regional blood flow in the pig-tailed monkey.

28. Reed, R.D.
Physiology. University of California, Berkeley, December 1977.
The effect of high altitude on pyridine nucleotides and adenosine phosphates in the liver of the rat.

29. Barnard, P.A.
Physiology. University of California, Berkeley, December 1977.
Whole body oxyhemoglobin affinity and red blood cell metabolism at sea level and high altitude in pig-tailed monkeys.

30. Husseini, W.K.
Physiology. University of California, Berkeley, June 1980.
Thyroid function at high altitude in the monkey, Macaca nemestrina

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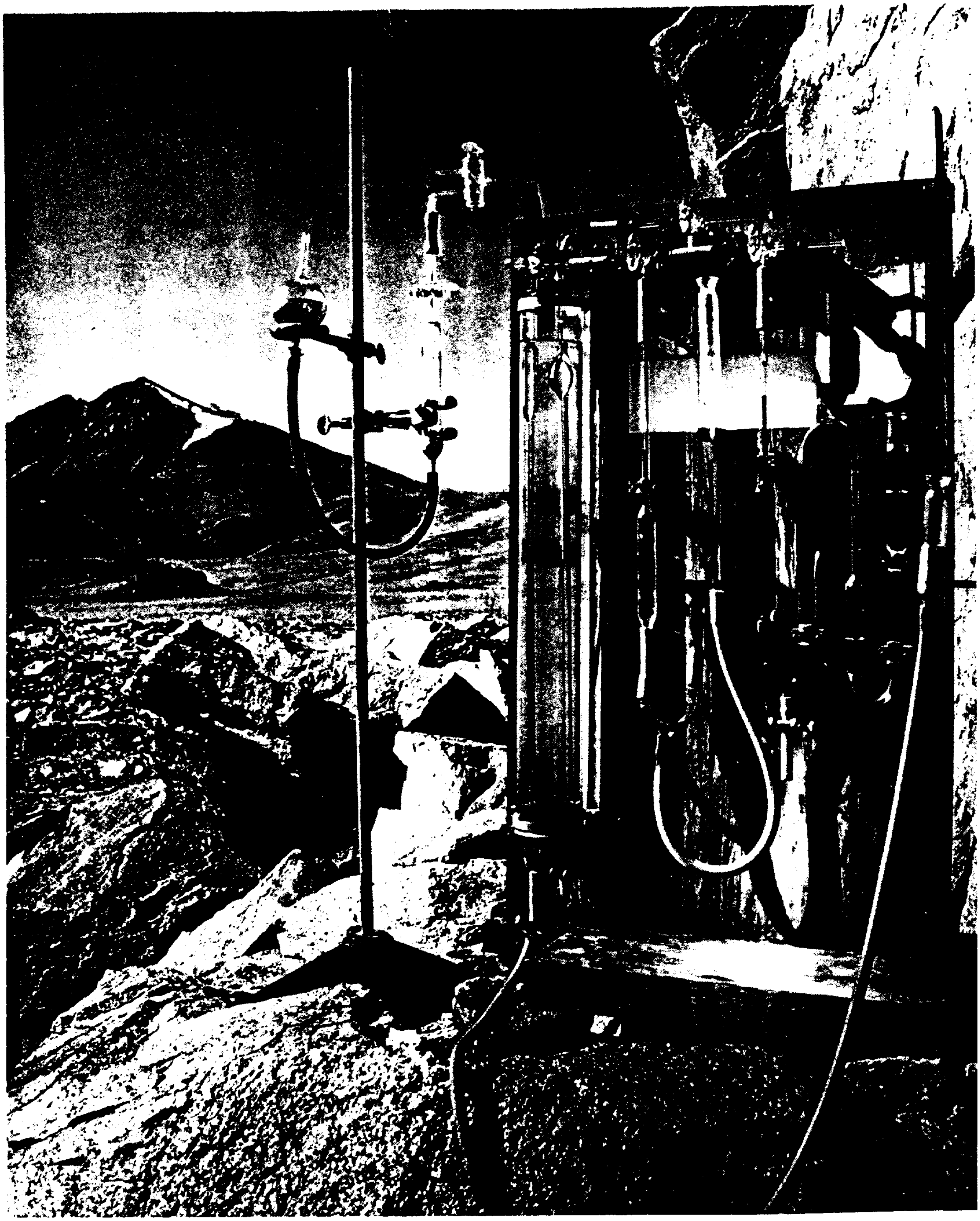
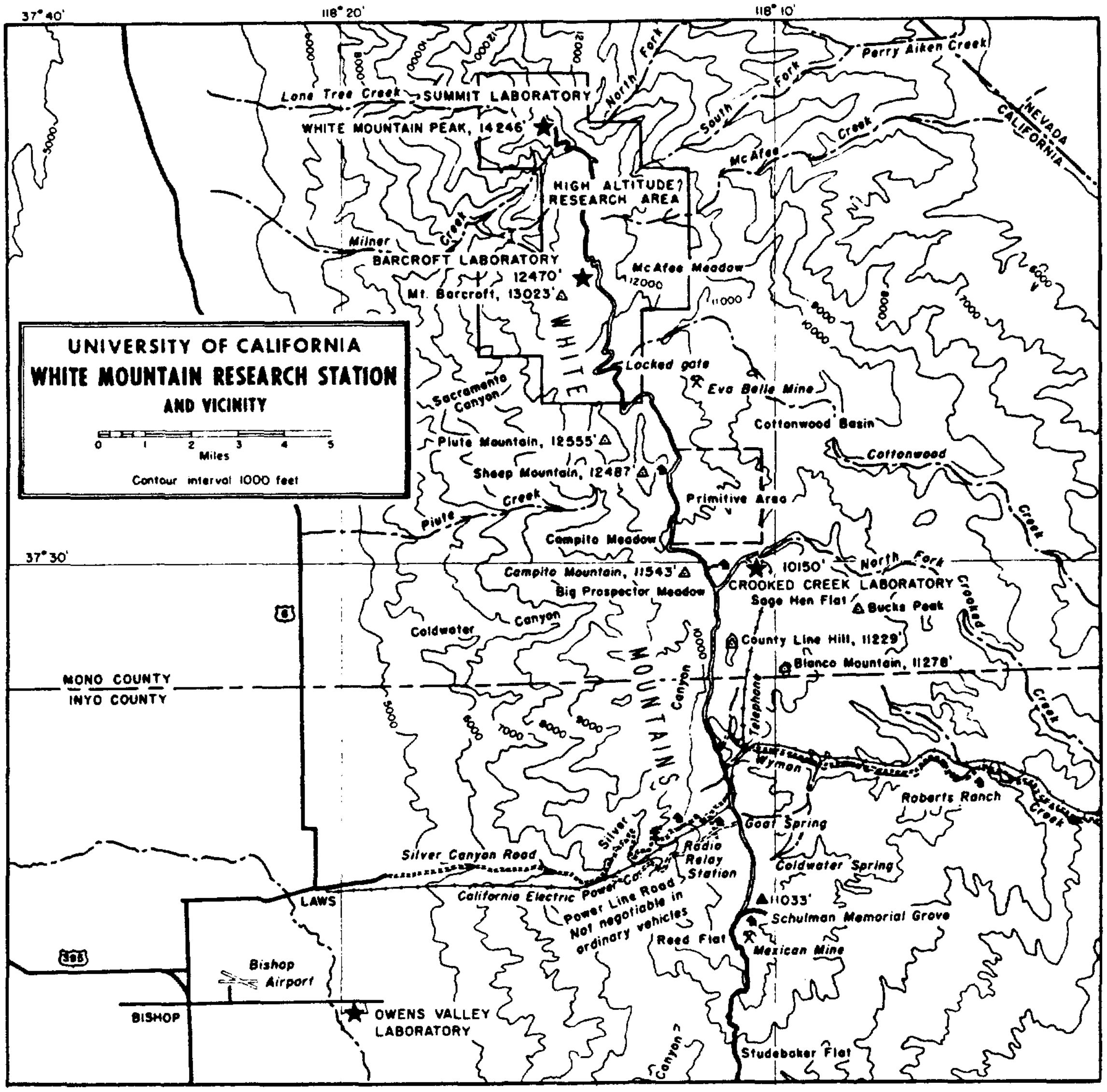


Above: gas analysis apparatus on White Mountain Peak.
Cover photo: White Mountain Peak from distant rock outcropping.



A history of the first 25 years
of the WHITE MOUNTAIN
RESEARCH STATION by some
of the scientists who made that history

Where It Is and Why

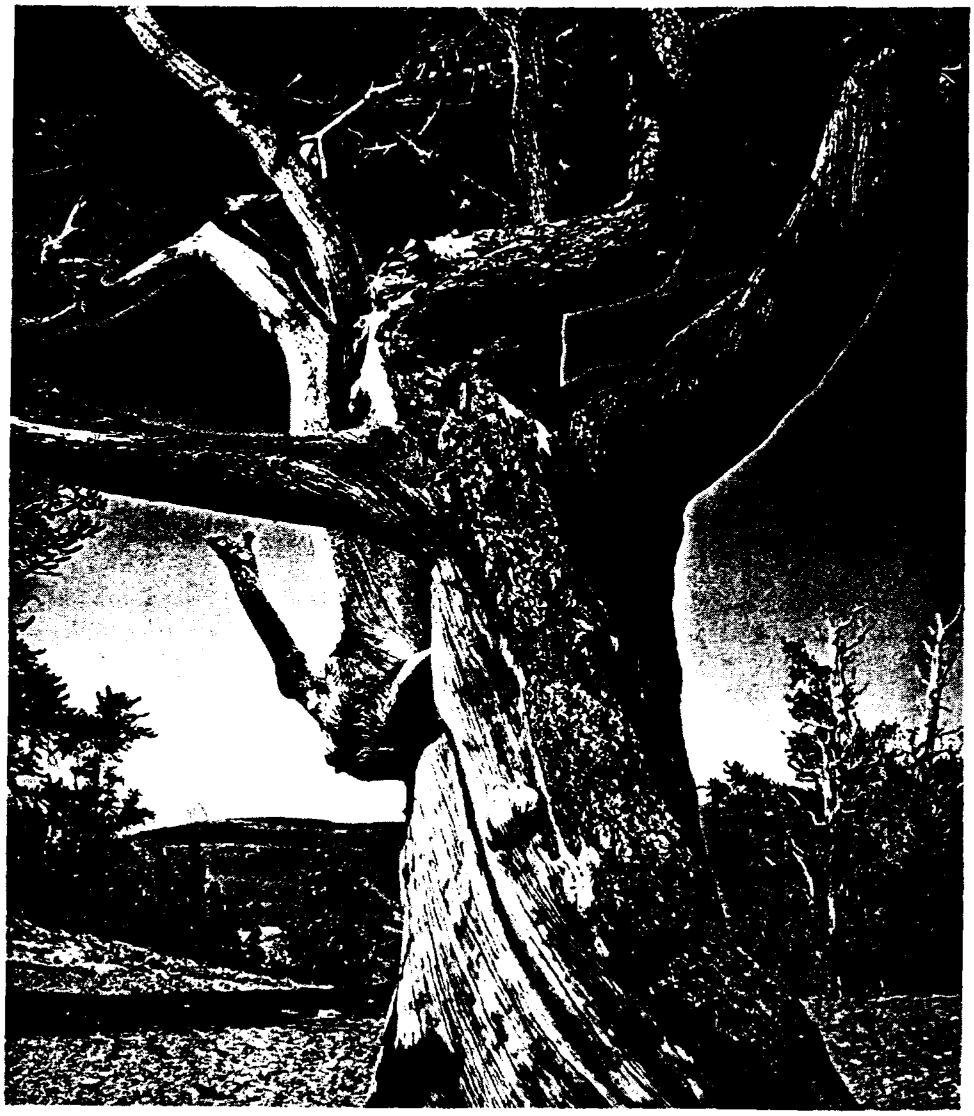
The White Mountain Research Station is a statewide organized research unit of the University of California, established for two purposes: (1) to provide laboratory facilities for any qualified research investigator who wishes to utilize the high-mountain environment in his work; and (2) to serve as a teaching facility for field courses conducted in the region.

Located in the vicinity of Bishop, California, the station comprises four separate laboratory sites — the Owens Valley Laboratory, 3 miles east of Bishop at an elevation of 4,050 feet above sea level; the Crooked Creek Laboratory on the White Mountain Range northeast of Bishop at an elevation of 10,150 feet; the Barcroft Laboratory at an elevation of 12,470 feet; and the Summit Laboratory atop White Mountain Peak at an elevation of 14,250 feet. The three laboratories above 10,000 feet are within the Inyo National Forest, and their operation is subject to regulations of the U. S. Forest Service as well as those of the University of California.

The Station laboratories are manned the year round by a permanent staff of eight persons under supervision of the Assistant Director. Administrative headquarters and the office of the Director are located at the Environmental Physiology Laboratory, University of California, Berkeley, which also serves as a site for sea-level control studies for some of the research performed at high altitude.

General operational policy for the Station is set by the President's Advisory Committee for the White Mountain Research Station, which includes faculty representatives from every campus of the University. The Director's Advisory Committee for Astronomy provides guidance for administration of astronomical research activities.

In the 25 years of its existence, several hundred scientists have used the Station laboratories and have been provided with food and lodging during their stay. These investigators have conducted research in a variety of fields in the agricultural, biological, and physical sciences, and have come to the Station from universities and colleges, from government laboratories, and from industrial research laboratories located both in this country and abroad. The Station facilities also have been utilized by several hundred undergraduate students enrolled in field courses conducted at the Station by a number of academic institutions.



Bristlecone pine with Sierra Nevada in distance.

Research . . . occasionally above "Cloud 9"

It would be an honor in any event to be asked to write the preface to this fascinating history, but for me it is a very special pleasure, because my ties to the White Mountain Research Station go back so far. In a way, they go far beyond the actual establishment of the Station, for it was as an undergraduate at the University of Arizona in the early Thirties that I took the first step which eventually would lead me to the top of White Mountain. I was an economics major, but somehow I made the leap across the disciplinary chasm between "the dismal science" and Arizona's unique Laboratory of Tree-Ring Research and developed into a pretty fair amateur dendrochronologist. It's an interest I never lost, though over the next four decades I rarely had the time to follow it closely.

To a dendrochronologist, age is all-important, and there is no living organism in the world older than the bristlecone pines such as have been standing on the White Mountain Range for many thousands of years. Some individual trees near the Station are over 4,600 years old, and while they cannot be said to be going strong, they cling tenaciously to life in an almost unbelievably hostile environment. When you first come upon their grey and gnarled forms, it requires some effort to recognize that they are in fact alive. Once you know it, however—and it is the kind of knowledge that is more than intellectual—once you fully comprehend their near timelessness, it becomes even harder to believe they will ever die. The bristlecones are as close to immortality as we are privileged to get. It is an humbling experience.

Thus it was that in the summer of 1969 I came to combine business and pleasure with a trip to review the operations of the White Mountain Research Station and to renew my acquaintanceship with the bristlecone pine. I found both in splendid condition. My enthusiasm resulted in another trip the following year and, no doubt, the invitation to include these thoughts in this history of the Station. From any vantage point it is an impressive story: twenty-five years of high-altitude research from astronomy to zoology, from human physiology to plant ecology, twenty-five years of tough and demanding work to establish a first-class research facility on the inhospitable top of the world. Professor Pace and his colleagues deserve the highest praise for their accomplishments and for making the effort to record them in such readable fashion. It's a real success story, and I am proud to be a small part of it.

Charles J. Hitch
President of the University

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Arthur H. Smith, Professor of Animal Physiology and Physiologist in the Experiment Station, University of California, Davis.

Members

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Robert Galambos, Professor of Neurosciences, University of California, San Diego.

Ralph H. Kellogg, Professor of Physiology and Vice Chairman of the Department, University of California, San Francisco.

Harold A. Mooney, Associate Professor of Botany, Stanford University, California.

Emil M. Mrak, Chancellor Emeritus and Professor Emeritus of Food Science and Technology, University of California, Davis.

Eric T. Pengelley, Professor of Biology, University of California, Riverside.

Robert Em. Smith, Professor of Physiological Sciences, University of California, Davis.

Paola S. Timiras, Professor of Physiology and Director of Medical Option, Health Sciences and Medical Education, University of California, Berkeley.

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David D. Cudaback, Associate Research Astronomer, Radio Astronomy Laboratory and Lecturer in Astronomy.

John E. Gaustad, Associate Professor of Astronomy.

William D. Gwinn, Professor of Chemistry.

Carl E. Heiles, Associate Professor of Astronomy.

John G. Phillips, Professor of Astronomy and Chairman of the Department.

George C. Pimentel, Professor of Chemistry.

Paul L. Richards, Professor of Physics.

Charles H. Townes, University Professor.

Harold F. Weaver, Professor of Astronomy.

IN MEMORIAM

Warm and grateful remembrance is hereby expressed for the significant contributions to high-mountain science and development of the White Mountain Research Station made during their lifetimes by:

Professor Robert W. Bullard, 1929–1971
Indiana University

Mr. Ewen H. Connolly, Jr., 1936–1970
Graduate student, University of California, Berkeley

Professor Emeritus Frank G. Hall, 1896–1967
Duke University

Dr. Julius T. Hansen, 1921–1973
Research Physiologist, Central Intelligence Agency

Professor Raymond J. Hock, 1918–1970
University of Nevada, Las Vegas

Dr. Kenneth W. Ramsey, 1914–1961
Veterinarian

Professor Edmund Schulman, 1908–1958
University of Arizona

Dr. J. Edward Spoon, 1930–1968
Veterinarian

Mr. Charles E. Wilson, 1920–1971
University of California, Retired

ACKNOWLEDGMENT

The major responsibility for the preparation of this commemorative publication in its final form was in the hands of Professors Ralph H. Kellogg, Arthur H. Smith, and Paola S. Timiras. Our sincere appreciation is extended to each of them.

The compilation and final typescript of its bibliography was handled with consummate skill by Miss Elizabeth M. Nissen.

1973

CONTENTS

A History, *Nello Pace* 9

The Men of Vision and Faith 18

Avian Physiology, *Arthur H. Smith* 19

Studies of Native Animals, *Raymond J. Hock* 23

Cardiorespiratory Physiology, *Ralph H. Kellogg* 27

Endocrinological Studies, *Herbert H. Srebnik* 31

Neurobiological Studies, *Paola S. Timiras* 33

Metabolic Studies, *F. Duane Blume* 36

Plant Ecological Research in the White Mountains, *Harold A. Mooney* 38

Geological Studies, *Valmore C. LaMarche, Jr.* 41

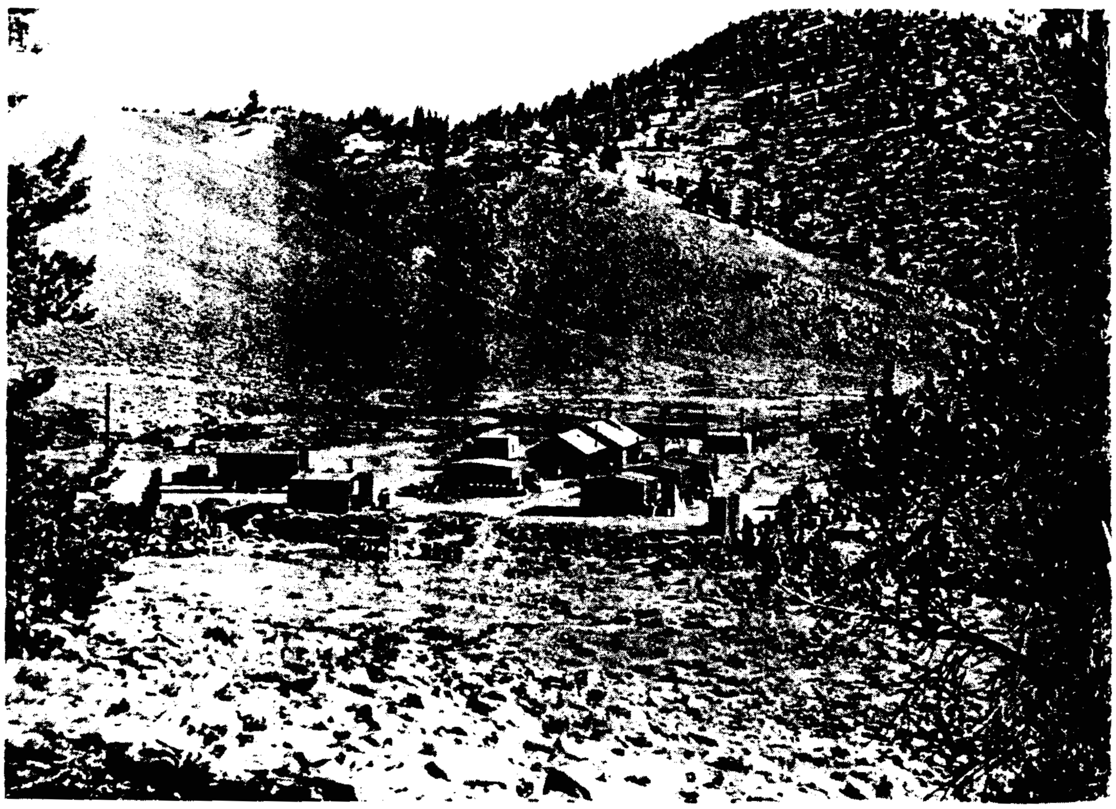
Physical Studies, *Ralph A. Nobles* 42

Astronomy and Meteorology at White Mountain, *David D. Cudaback* 44

Publications Concerning Work Performed at the White Mountain Research Station to January 1, 1973 47

Advanced Degrees Involving Thesis Research Done at White Mountain Research Station up to July 1, 1973 59

Right: Crooked Creek Laboratory framed by bristlecone pines. July, 1958.



A HISTORY

Nello Pace[1]

The formal establishment of the White Mountain Research Station on September 1, 1950, marked the evolution and convergence of two independent lines of scientific interest. First, the need of astronomers and astrophysicists to obtain observatory sites that would provide the best seeing conditions with a minimum of atmospheric interference. Second, the need of biologists to undertake a careful exploration of the ecology peculiar to the high-altitude environment and the physiological processes that are involved in acclimatization.

Thus it was that in the middle 1930's Dr. Ira Sprague Bowen, then Professor of Physics at the California Institute of Technology and later Director of both the Mount Wilson and Palomar observatories, called attention to an astronomical site in the White Mountain Range of east-central California, where the unusually low humidity coupled with high land elevation offered great potential for an observatory.

This mountain range forms the east wall of the great Owens Valley in its northern half and is geologically quite distinct from the Sierra Nevada. Because of its geographical position as the first of the Great Basin ranges just east of the Sierra Nevada it receives far less annual precipitation (about one quarter) than that falling at comparable elevations in the Sierra Nevada and has been called the "rain shadow" of these mountains. The White Mountain Range reaches its highest point at White Mountain Peak, 14,246 feet above sea level—the third highest point in California and the nineteenth highest in the contiguous 48 states. At this elevation, 42 per cent of the earth's atmosphere lies beneath the peak.

Below: Paul J. Manis, Operations Manager, discussing policy matters with Professor Nello Pace, Director, at the Crooked Creek Laboratory. Summer, 1960.

Before 1950

Research during World War II at the U. S. Naval Ordnance Test Station, Inyokern, California, led to the development of infrared-seeking missiles, which by 1948 required high-altitude field tests of the sensors. Dr. Bowen, remembering his personal explorations of the White Mountain Range in the 1930's, suggested a site at the head of Crooked Creek. Through the efforts of Commander Eugene Bollay of the Office of Naval Research, by October, 1948, a small frame building to provide living quarters had been built in a small sheltered valley at an altitude of 10,150 feet, and an observing site had been established on the east rim of the valley at 10,600 feet. A pre-existing network of old mining roads was improved to provide four-wheel drive access to the area, and a commercial telephone land-line was installed. All of these construction projects were carried out by the U. S. Navy under special use permits issued by the U. S. Forest Service.

In the course of the next two years, the Crooked Creek installation was manned and operated the year around, and much classified research was carried out. In addition, several unclassified research projects were initiated: Among these were cosmic-ray studies by Professors Robert B. Brode and William B. Fretter of the Department of Physics, University of California, Berkeley; cosmic-ray studies by Professor Carl D. Anderson of the Physics Department, California Institute of Technology; a study of the velocity of sound at altitude by Professors Vern O. Knudsen, Leo P. Delsasso and Robert W. Leonard of the Department of Physics, University of California, Los Angeles; and a study of the astronomical seeing qualities of the atmosphere above the White Mountains by Professor Fritz Zwicky of the Astronomy Department, California Institute of Technology and Dr. Walter O. Roberts of the High Altitude Observatory, Boulder, Colorado. This last project clearly demonstrated that Professor Bowen's earlier predictions of the superior characteristics of this general area for astronomical work were indeed correct.

Another development during the two-year period from 1948 to 1950 was the extension of the rough dirt road northward along the crest of the range to a flat plateau at an elevation of 13,200 feet, just below the

[1] Nello Pace is Director of the White Mountain Research Station and Professor of Physiology, University of California, Berkeley.

Left photo: some of the constructors of the Barcroft Laboratory. Front row, left to right: J. T. Hansen, R. B. Choate, J. V. Shriber, Professor S. F. Cook, F. L. Schaeffer, B. E. Vaughan, K. L. Jackson and D. Green. Rear row, left to right: W. F. Munch, F. D. Meskauskas, D. H. Wiltsie and Professor Nello Pace. September, 1951. Right photo: Donald J. Badger and Julius T. Hansen, graduate students, U. C. Berkeley, in the kitchen, Crooked Creek Laboratory. October, 1957.

summit pyramid of White Mountain Peak. Several laboratory trailers were emplaced for investigations there as well as at Crooked Creek. The cosmic-ray physicists from the University of California, Berkeley also installed a laboratory trailer on the slope of Sheep Mountain at an elevation of 12,000 feet about midway between Crooked Creek and the end of the road.

Hypoxia research needed

The years of World War II and thereafter saw a massive acceleration of research activity in the field of high-altitude physiology. Because large numbers of aviators were faced with exposure to the effects of hypoxia, or low oxygen, an urgent need developed to understand the physiological mechanisms involved in adaptation to high altitude. Many low-pressure chambers were built at that time in the United States, both for purposes of training and physiological research. It gradually became apparent, however, that the process of high-altitude acclimatization is a slow one, requiring weeks or months for completion, and the low-pressure chamber is unsuitable for long-term studies of the effects of hypoxia. A high-altitude research facility was needed not only to permit physiological studies of chronic hypoxia on sea-level natives taken to high altitude, but studies were also needed of native living forms which have successfully adapted to the high-mountain environment over many generations. For these purposes, sophisticated modern laboratory facilities were required in close juxtaposition with the undisturbed high-altitude flora and fauna in their native habitat.

In 1948, as Assistant Professor of Physiology at the University of California, Berkeley, and former Head of the Physiology Department of the U. S. Naval Medical Research Institute, Bethesda, Maryland during World War II, I began surveying possible sites for a high mountain biological research facility. Factors of importance were year-round access, a rich native flora and fauna characteristic of the high-mountain environment, and nearness to established academic centers of research located at sea level where base-line studies could be conducted. I considered a number of locales, such as the Peruvian or Bolivian Andes, the Mexican highlands in the vicinity of Mt. Orizaba, the Alaskan mountains (notably Mt. Wrangell) and the mountains of Hawaii (Mauna Loa and Mauna Kea). However, it was quickly obvious that economics dictated a site within the continental United States, excluding Alaska. On this basis, local possibilities were examined in detail. The Colorado Rockies were ruled out because of their great distance from sea-level laboratories, and because of the severity and length of the winter season, which makes year-round operation extremely difficult.

A tentative decision was made to exploit the stone structure atop Mt. Whitney, built originally in 1912 by C. G. Abbot of the Smithsonian Institution for solar observations. Preliminary conversations with the U. S. National Park Service, which has jurisdiction over this site, indicated that our utilization of this building was feasible. Then early in 1949, officials of the Sierra Club drew my attention to the White Mountains as a much more favorable location for a high-altitude biological research area.

That summer, in the company of William E. Siri, Biophysicist in the Donner Laboratory of the University of California, I made a comparative study of the two sites. The uniquely favorable features of the White Mountain region promptly led me, in collaboration with Professor S. F. Cook, also of the Department of Physiology in Berkeley, to submit a research proposal to the Office of Naval Research seeking to establish a high-altitude laboratory some ten miles

Left: William Roche, Senior Maintenance Man, during a visit by his grandson to the Barcroft Laboratory. October, 1957. Right: summit of White Mountain from the plateau just above the Barcroft Laboratory. August, 1958.

north of the U. S. Naval Ordnance Test Station installation at Crooked Creek. The proposal was sponsored by Professor John H. Lawrence, Director of the Donner Laboratory, because of his long-standing interest and research experience in high-altitude physiology.

Ideal research site

The new site was well above timber line near a natural spring at an elevation of about 12,500 feet. It was particularly suitable for research on the physiological effects of hypoxia and was in the midst of a rich, unspoiled ecological zone of the high-alpine type. The pioneering activities of the Navy group during the preceding year had demonstrated that year-round access was entirely possible, and their presence at the lower elevation of Crooked Creek was deemed most handy.

After a site visit in July of 1950, Dr. William V. Consolazio, Head of the Physiology Branch of the Office of Naval Research, approved the proposal. However, upon leaving the Crooked Creek installation, we learned that the U. S. Naval Ordnance Test Station research activities being completed, the installation was to be dismantled and removed in a few weeks. Dr. Consolazio and I quickly conferred with authorities in Inyokern and reached an agreement to have the buildings and equipment at Crooked Creek transferred to the Office of Naval Research rather than removed. In turn, the Office of Naval Research authorized the University of California, Berkeley, through Professor Cook and me to continue to operate the Crooked Creek installation and to proceed with the development of another installation at the higher elevation 10 miles north. Dr. Orr E. Reynolds, then Director of the Biology and Medicine Division of the Office of Naval Research, was also importantly involved in the decision to proceed with this development.

On September 1, 1950, the property transfer papers were signed, and the University of California began operation of the White Mountain Research Station for the Office of Naval Research, as a national facility open to any scientific investigator wishing to pursue research in the high-mountain environment. I was designated as Director of the Station, and Mr. Paul J. Manis was employed as local Operations Manager. Mr. Manis had wintered over at Crooked Creek in 1949–1950 as part of the University of California, Los Angeles, sound velocity project, and was familiar with the maintenance operations of the Crooked Creek Laboratory. The existing Special Use Permits originally issued by the U. S. Forest Service to the Commandant of the Eleventh Naval District were transferred to the Commandant of the Twelfth Naval District. Mr. Robert A. San Souci, Business Manager of the Donner Laboratory, was of great assistance during this early period.

Barcroft Laboratory started

The winter of 1950–1951 passed uneventfully, and in the summer of 1951 construction of the Barcroft Laboratory was started at an altitude of 12,470 feet on the east slope of an unnamed peak, 13,040 feet high, six miles south of White Mountain Peak. A two-story quonset building, 40 x 100 feet, was erected. It was designed to provide laboratory and living accommodations for 24 investigators, in contrast to the Crooked Creek Laboratory which could accommodate only ten. Electric power, as at Crooked Creek, was supplied by diesel generators.

Mr. Robert B. Choate, Jr., was the engineer in charge of construction, and his work crew consisted principally of graduate students and faculty from

Above: Summit Laboratory from the air.

the University of California, Berkeley. Particularly noteworthy were the personal efforts of Professor Sherburne F. Cook of the Department of Physiology, and of Dr. Julius T. Hansen, then a graduate student in Physiology. The other stalwarts comprising this high-level pioneering group included G. Harry Anderson, James A. Bassham, Carl F. Cramer, Joseph F. Garcia, Constantine M. Glafkides, Donald Green, J. Patrick Hannon, Kenneth L. Jackson, David Jensen, John H. Kilbuck, Frank D. Meskauskas, Peter G. Miljanich, William F. Munch, Frederick L. Schaffer, John C. Schooley, Jack V. Shriber, Burton E. Vaughan and David H. Wiltsie.

The basic structure was completed in October, 1951, and was occupied by a skeleton maintenance staff. At this time, Evelyn J. Moreland was employed in Berkeley as the first Business Officer of the Station, a position she held until July, 1956.

The winter of 1951–1952 proved to be one of the most severe on record in California, and the Barcroft Laboratory was closed down until the following summer. It opened again in June of 1952 and has operated continuously since then. Great credit must be given to Mr. William Roche who, during the first 12 years of operation of the Barcroft Laboratory was its Senior Maintenance Man, and who developed many of the special procedures required for continuous operation in this exceedingly harsh environment.

Agreement restricts traffic

A development of vital importance to the research objectives of the Station occurred on November 16, 1951: the signing of a Cooperative Agreement between the U. S. Forest Service and the U. S. Navy, setting aside 20 sections of the Inyo National Forest on the highest part of the White Mountain Range for high-altitude research purposes. The entire 20-square-mile research area lay above 12,000 feet, well above timber line, and included the site of the Barcroft Laboratory.

The major feature of the Cooperative Agreement was that vehicular traffic into the research area was to be restricted to the minimal official travel necessary to support the ongoing research activities. It was recognized in 1950, and it is equally true today, that unregulated vehicular traffic into the area would quickly and irreversibly destroy the delicate biological balance of this resource, which exists under marginal environmental conditions at best. Because the locale involved combines extreme elevation with the climatic features of the Great Basin and the Southwestern Desert, and at the same time lies within 5 to 30 miles of the distinctive Sierra Nevada ecological province, it represents a transitional region of unique importance. The loss of this natural ecology would remove much of the fundamental justification for continued operation of the Station.

Another problem created by unregulated entrance into the research area is that of the broad-spectrum electromagnetic interference generated by the ignition systems of motor vehicles. Such interference is a serious impediment in carrying out many types of measurements in both infrared and radio astronomy. One of the important features of the White Mountains, as noted earlier, is their unique potential for certain types of astronomy. As a result of a detailed survey carried out in 1967 and 1968 by personnel of the Space Sciences Laboratory, University of California, Berkeley, it is now evident that the water vapor content above this range is less than that at any other site in the world thus far surveyed. The relative absence of atmospheric water vapor, together with the reduced density of the atmosphere itself and freedom from dust, stray night light, and artificial electromagnetic emissions, make the White Mountain Research Area an extraordinarily valuable site for astronomical observations in the wave-length region from 1 micron in the near infrared to 2 to 3 centimeters in the short radio wave portion of the electromagnetic energy spectrum.

Professor Charles H. Townes, Professor at Large in the Department of Physics, University of California, Berkeley, points out that the random electromagnetic emissions from vehicle ignition systems operating in the general area of infrared and radio telescopes can be picked up by the sensitive electronic circuits used for many experiments which require very high amplification, thereby interfering seriously with such

Below: Fenton C. Kelley, graduate student, U. C. Berkeley, in the doorway of Summit Laboratory. Diamond-shaped target above roof used by Army surveyors to revise topographical quadrangles in this neighborhood. August, 1958.

observations. He also points out that the National Radioastronomy Observatory at Greenbank, West Virginia, has had to institute careful control of the electromagnetic environment, in particular the restriction of motor vehicle operation in the general vicinity of the radio telescope installations.

Station policy set

To resume the narration of the historical development of the Station: In 1952 Robert Gordon Sproul, President of the University, appointed an advisory committee for the White Mountain Research Station that played a key role in shaping the operational policies of the Station, as well as in providing advice both to the University administration and to the Federal funding agencies.[2] Particular acknowledgement also must be made to President Sproul and Regent Donald H. McLaughlin for their confident and effective support of the Station in its first years.

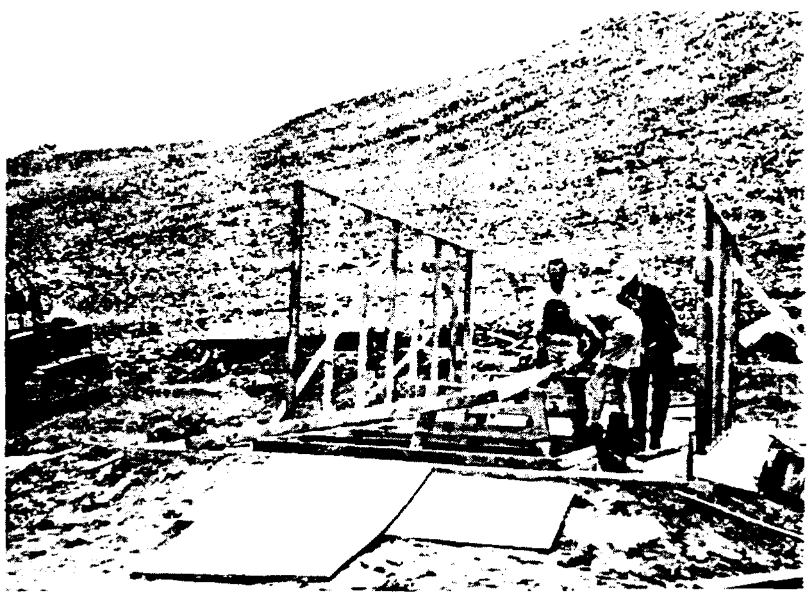
Also, in 1952, the National Science Foundation and the Rockefeller Foundation joined the Office of Naval Research in providing funds for maintenance support of the Station. In 1955, the Regents of the University of California began to provide financial support to balance the gradual withdrawal of support by the Rockefeller Foundation; by 1958 the Regents had completely supplanted the Rockefeller Foundation in contributing support to the Station.

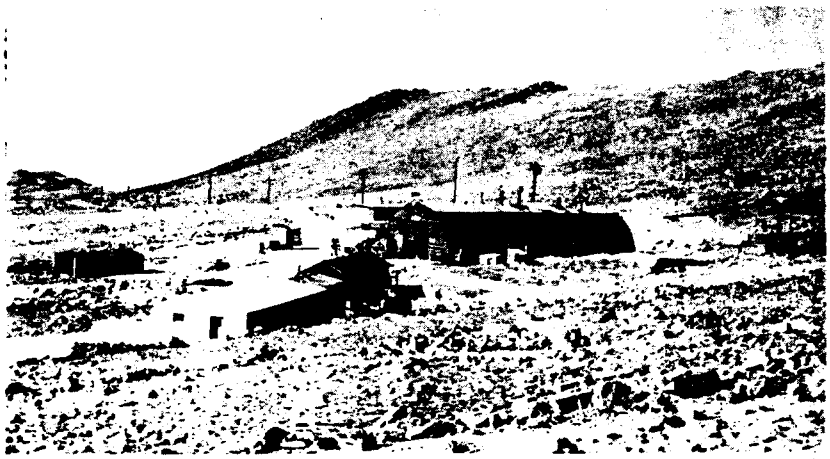
During the summer of 1953, Professor Edmund Schulman of the Laboratory of Tree-Ring Research, University of Arizona, made the first of his many visits to the Station to study the longevity of the local bristlecone pines. In the next few years until his untimely death in 1958, Professor Schulman and his colleagues, Professors W. G. McGinnies, Harold C. Fritts, and C. Wesley Ferguson were able to discover living specimens of bristlecone pines over 4,600 years old. The stand of trees containing these specimens has been designated by the U. S. Forest Service as the Edmund Schulman Memorial Grove in recognition of his discovery of the world's oldest living organisms. It is of significance that the University of Arizona group, by also examining fallen, dead trees in the area, has now been able to construct a continuous tree-ring chronology for the past 7,500 years.

In May of 1954, the U. S. Board of Geographic names formally approved my suggestion to name the 13,040-foot peak just south of White Mountain Peak in memory of the pioneer high-altitude physiologist, Sir Joseph Barcroft, of Cambridge University. Professor Barcroft had worked out the fundamental

[2] Professor Sherburne F. Cook was chairman. The members were Professors Leslie L. Bennett, Raymond B. Cowles, Leo P. Delsasso, William B. Fretter, Max Kleiber, A. Starker Leopold, Samuel Lepkovsky, Emil M. Mrak, Robert Em. Smith and George F. Stewart, and Mr. James M. Miller and Mr. Robert A. San Souci of the University administration. This committee functioned unchanged until 1960, at which time a gradual rotation of membership was begun by President Clark Kerr. Besides the incumbent members of the committee, others who have served are Professors George A. Bartholomew, Jr., Lincoln Constance, Steven M. Horvath, Robert W. Leonard, Peter R. Morrison, Hermann Rahn, Per F. Scholander, Robert C. Stebbins, S. Marsh Tenney, and Charles H. Townes.

Left: Donal J. Reed and Joachim F. Wohlwill, graduate students, U.C. Berkeley, preparing urine samples in the kitchen for subsequent analysis. Summit Laboratory, August, 1956. Below: D. Glenn Reck and George Bond, veterinary students, and Kenneth Ramsey, undergraduate, U. C. Davis, constructing the rat building. Barcroft Laboratory, July, 1955.






Left: Barcroft Laboratory from the northeast, Sierra Nevada in the distance across the Owens Valley. Dog building, Arctic Hut (for comparative physiology of native mammals), poultry building, women's main quonset. Summer, 1960. Right: Robert F. Delker, pilot, with Bell 47G-3B-1 helicopter atop White Mountain Peak. July, 1966.

physiological properties of blood hemoglobin and had elucidated many of the characteristics of the high-altitude acclimatization process in man. The Barcroft Laboratory is on the east slope.

During the first half of 1954, I accompanied the California Himalayan Expedition to Nepal as deputy leader. We wanted to reach the summit of Mount Makalu, the world's fifth-highest peak whose elevation is 27,894 feet above sea level. Exceptionally poor weather limited the climbing activities to a maximum altitude of 23,500 feet, but considerable data were gathered on the physiological effects of extreme high altitude on man to correlate with the effects observed at White Mountain. The results served to confirm the earlier premise that the altitudes of the Station laboratories were sufficient to evoke all the qualitative components of the high-altitude acclimatization process.

A 14,250-foot high laboratory

A special grant by the National Science Foundation in 1955 permitted extension of the dirt road from its earlier terminus on the plateau at 13,100 feet to the summit of White Mountain Peak, and the construction of a small laboratory building, 15 x 30 feet, on the summit at an elevation of 14,250 feet. Particular credit is due Professor Ralph H. Kellogg, Department of Physiology, University of California, San Francisco, for his active participation in the construction of this building to ready it for its first research. The stone building is known as the Summit Laboratory, and can house four investigators comfortably. Along with the Barcroft Laboratory at 12,470 feet, it also lies within the boundaries of the original 20-square mile Research Area.

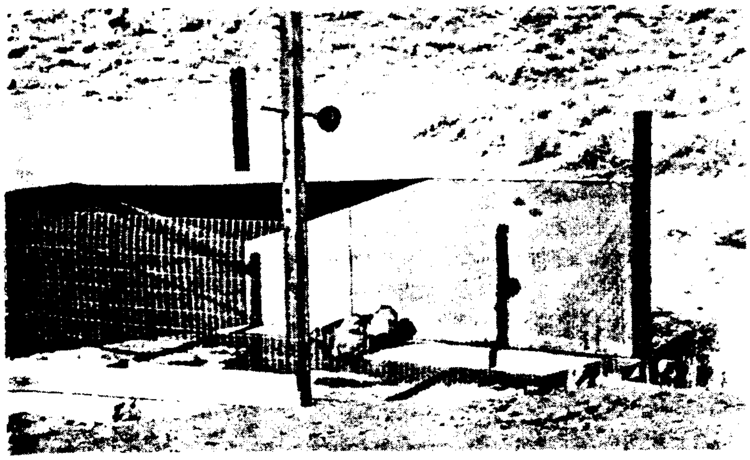
In the summer of 1955 two more frame buildings were erected at the Barcroft Laboratory site—one to house small experimental laboratory animals such as mice, rats, guinea pigs and rabbits, and the other to house an experimental flock of chickens, which has been bred there continuously since 1955 by Professor Arthur H. Smith of the Department of Animal Physiology, University of California, Davis.

Another frame building was erected at the Barcroft Laboratory in 1956 to serve as quarters for visiting female investigators. In May of that year, Joseph H. Wentworth replaced Paul Manis as Operations Manager, while the latter was on sick leave. Mr. Manis returned to his post in October, 1957. In July, 1956, Evelyn Moreland resigned, and was replaced by Mr. Mun Q. Mah as Business Officer of the Station.

In 1957, a National Science Foundation grant of $132,000 was gratefully received for the construction of a 12,000-volt commercial electric power line 16.4 miles long to supply the three laboratory sites. The Regents of the University of California also made a special allocation of $25,000 to supplement the National Science Foundation grant. The line was designed by Mr. Carl T. Grauer, Electrical Power Engineer for the Lawrence Radiation Laboratory, Livermore, who also supervised its installation. Although the line to the summit of White Mountain Peak was completed by the fall of 1957, by the end of that winter it became evident that severe icing conditions above 12,500 feet made an overhead power line impractical for the last four miles of the line from the Barcroft Laboratory to the Summit Laboratory. Future plans call for laying underground cable to provide commercial electric power to the Summit Laboratory.

Owens Valley Laboratory at 4,000 feet

A building was leased in 1958 in the town of Big Pine, California, in the Owens Valley to serve as a low elevation (4,000 feet) laboratory, as local headquarters for the Station, and as a storage warehouse.



Above: Harbor seals at the Crooked Creek Laboratory. October, 1971.

In October of the same year, Mun Q. Mah left the employ of the Station to return to graduate school, and was replaced by Mr. Harry E. Pike as Business Officer of the Station.

A special appropriation of $73,000 was granted from the Office of Naval Research to improve the dirt road between the Crooked Creek Laboratory and the Barcroft Laboratory in 1959. In addition, a frame building with attached outdoor runs was constructed to house dogs for research purposes at the Barcroft Laboratory, and in 1960, a building was erected there to house wild native mammals for study.

Dr. Raymond J. Hock joined the Station staff as Research Physiologist and the first resident scientist. Dr. Hock instituted a research program on the comparative physiology of the native mammals of the area in collaboration with Professor Robert Em. Smith of the Department of Physiology, University of California, Los Angeles.

In 1961 three more buildings were erected at the Crooked Creek Laboratory—a dormitory, a research poultry house, and a vehicle maintenance shop.

A small astronomical observatory was constructed in 1962 by Station personnel for Dr. Bruce Murray and Dr. James Westphal of the Lunar Research Laboratory, California Institute of Technology, on a site at 12,800 feet elevation near the Barcroft Laboratory. From this year until 1965, the U. S. Public Health Service began making a small contribution to the financial support of the Station. Also, a nine-acre site was acquired on a long-term lease basis from the City of Los Angeles to provide for the construction of a new headquarters and low-level laboratory in the Owens Valley. The site selected was 3.5 miles east of Bishop, California, on East Line Road.

NASA support

The winter of 1962–1963 was again severe, and resulted in major damage to the power line supplying the Barcroft Laboratory. However, 1963 saw the beginning of National Aeronautics and Space Administration (NASA) support for maintenance, which included funds for repair of the power line and for the operation of a high-altitude helicopter for Station logistics. Negotiations with the City of Los Angeles resulted in an increase from 9 to 25 acres of the leased site in the Owens Valley; this area was fenced, and a water well was drilled on the site. In the fall, the California Institute of Technology Lunar Research Laboratory moved its astronomical observatory from the 12,800-foot elevation to a site at 10,600 feet just east of the Crooked Creek Laboratory.

Robert M. Lloyd, then a graduate student in botany at the University of California, Berkeley, was employed by the Station in 1963 to carry out a botanical survey of the White Mountain Range. In the summer of 1964, Richard S. Mitchell, also a graduate student in botany, was employed to collaborate with Mr. Lloyd in completing the survey. Their specimens were filed in the Herbarium on the Berkeley campus, and a duplicate herbarium was established at the Crooked Creek Laboratory. Both subsequently received their doctorates in Botany. The results of their survey have now been published in book form under their authorship with the title *A Flora of the White Mountains, California and Nevada*, University of California Press, as the definitive botanical description of this important ecological region.

At the end of 1963, Mr. Paul J. Manis, who had served with distinction as Operations Manager of the Station since its beginning in 1950, retired. He was replaced by Mr. Charles E. Wilson in October of that year.

Helicopter service

The National Science Foundation phased out its maintenance support of the Station in 1964, in view of the major burden then being assumed by NASA. A Bell 47G-3B-1 helicopter was acquired in February, 1964, and, by the end of the year, had been flown more than 600 hours to altitudes up to 14,250 feet by Pilot Leonard A. Johnson at the Summit Laboratory. A standby electric generator building was added at the Barcroft Laboratory, and a hangar for the helicopter was built on the Owens Valley Laboratory site at 4,050 feet. In October, 1964, Dr. F. Duane Blume joined the resident scientific staff of the Station as Assistant Research Physiologist.

Several months later, a new helicopter pilot, unfamiliar with the White Mountain terrain and special operational constraints there, was unable to maintain lift and made a forced landing of the machine on a steep slope near the Crooked Creek Laboratory. He and his two passengers escaped without injury, but the helicopter overturned after they had left it, and was a total loss. The machine was replaced by August, 1965, with another Bell 47G-3B-1, and operations were resumed with Mr. Robert F. Delker as helicopter pilot. Three frame buildings were acquired from the U. S. Vanadium Corporation in Bishop, and were moved to the Owens Valley Laboratory site to provide office space, laboratory space, and experimental animal quarters in support of the high-altitude laboratories. At the end of 1965, Dr. Hock resigned from the Station staff, leaving Dr. Blume as the sole resident scientist.

Early in 1966 a pre-fabricated steel classroom building was erected at the Owens Valley Laboratory to provide a conference area. In addition, several University of California Extension Division courses were established, which were given on a regular, repeating basis under the administration of Dr. Blume.

The Station's second helicopter accident occurred in August of 1966. The Bell machine suddenly lost power on take-off from the Barcroft Laboratory, and the pilot and two passengers, one of whom was Mr. Charles E. Wilson, Operations Manager of the Station, received moderate to serious injuries when the machine made a crash landing. Mr. Harry L. Wells, Senior Maintenance Man at the Barcroft Laboratory, was specially commended for his prompt and effective first aid, which was credited with saving the lives of the victims of the accident. The injuries incurred by Mr. Wilson led to his retirement from the University, and Mr. Delker was named Operations Manager in his place.

An increase from 25 acres to 470 acres, including frontage along the Owens River, was negotiated with the City of Los Angeles for the Owens Valley leased site in March, 1967. A Hiller SL-4 helicopter, accommodating three passengers and pilot, was acquired in July, 1967, and has been operating continuously since then. Mr. Donald F. Buser, an FAA-certified helicopter mechanic, was employed at the same time to provide continuous preventive maintenance for the machine. Two storage buildings were erected in 1967 at the Barcroft Laboratory. In addition, the Space Sciences Laboratory of the University of California, Berkeley, erected an 8 × 10 feet insulated instrumentation building on the plateau site in the research area at an elevation of 13,200 feet just below White Mountain Peak.

Then, on April 1, 1969, Dr. Blume was appointed Assistant Director of the Station and assumed the responsibility for overall local administration. Mr. Michael N. Antoniou replaced Mr. Delker as helicopter pilot at the end of 1969, and Mr. Buser was appointed Operations Manager of the Station.

President Hitch visits

A highlight of the summer of 1969 was the first visit to the Station by a President of the University. In July of that year President Charles J. Hitch spent two days at White Mountain. The experience was apparently noteworthy, for he returned for another two days the following year, accompanied this time by Mrs. Hitch and President and Mrs. John C. Weaver of the University of Missouri. With President Hitch in 1969 was Dr. Dana K. Bailey, a lifelong friend and geophysicist with the National Bureau of Standards. Dr. Bailey is also an amateur botanist who became interested in the taxonomy of the group of pines which comprise the foxtail pines and bristlecone pines. As a result of his careful studies of these trees on mountain ranges of the Colorado Plateau and the Great Basin, as well as at White Mountain, he was able to show that the very old bristlecone pines of California and Nevada represent a separate new species which he named *Pinus longaeva*—now formally recognized as distinct from *P. balfouriana* and *P. aristata*.

In the spring of 1970, a pre-fabricated steel building was erected at the Owens Valley Laboratory to provide student dormitory space for 24 men and six women. One of the frame buildings at the site was altered to make kitchen and dining space available to the dormitory. During the summer of 1970, a new course, Wildlife and Fisheries Biology S101, was established by Dr. R. W. Brocksen and Dr. R. G. Schwab of the Department of Animal Physiology, University of California, Davis; the facilities were thus used for the first time.

A new scientific area

During the latter half of 1970 the 1951 Cooperative Agreement between the U. S. Forest Service and the U. S. Navy was replaced by a Classification Order under Secretary of Agriculture Regulation U-3, establishing the White Mountain Scientific Area. The new Scientific Area still includes both the Summit Laboratory and the Barcroft Laboratory, and embraces a total of approximately 5,010 acres of the Inyo National Forest along the highest portion of the White Mountain Range.

Simultaneously with the establishment of the White Mountain Scientific Area, Professor Gerard P. Kuiper of the University of Arizona published a critical review of high-altitude sites which would be favorable for infrared astronomical observations. In this paper he listed White Mountain as a potentially good site for such work. As a result of discussions with Professor Kuiper, I was encouraged to appoint an advisory committee on astronomy composed of interested members of the University of California, Berkeley, faculty with Professor George B. Field as chairman.

As a result of action by this committee, in January, 1971, Dr. David D. Cudaback, of the University of California Laboratory of Radio Astronomy, began a quantitative survey of the water vapor content and astronomical seeing qualities of the atmosphere above the Summit Laboratory. The survey, which extended over a period of 18 months, demonstrated that White Mountain is an exceptionally good site for infrared and submillimeter wavelength astronomical observations when compared with other high-mountain astronomical observatory sites. Well substantiated, therefore, was Dr. Ira Bowen's prediction in the 1930's of the potential importance of White Mountain as a major astronomical asset.

During the first six months of 1971, Dr. Blume carried on the tradition of White Mountain participation in Himalayan mountaineering expeditions by accompanying the International Himalayan Expedition to Mount Everest as its Oxygen Officer. Although the expedition was unsuccessful in its attempt to reach the summit by direct ascent of the Southwest Face, a diluter-demand oxygen supply system designed by Dr. Blume and me worked very well and permitted two of the climbers to remain continuously above 25,000 feet for 23 days with excellent oxygen economy.

High-altitude oceanography

The new field of "high-altitude oceanography" was initiated at White Mountain in the fall of 1971. In a collaborative experiment, Professor Robert W. Elsner of the University of California, San Diego, together with Dr. Arthur M. Kodama, of the Berkeley campus, and I transported two harbor seals (*Phoca vitulina*) to the Crooked Creek Laboratory, where the animals remained for three months. At intervals during their stay respiratory and hematological studies were made to determine the time-course and degree of high-altitude acclimatization in these marine diving mammals. A constant flow of fresh water was provided to the seals from the spring at Crooked Creek, and by all indications they tolerated their mountain sojourn exceptionally well.

Dr. Thomas A. Ledoux joined the Station staff as Assistant Director in October, 1972, replacing Dr. Blume who had resigned from the University that year. Dr. Ledoux has initiated a research program on the effects of the chronic hypoxia of high altitude on the reproductive process in mammals and birds, using the facilities of the Owens Valley, Crooked Creek, and Barcroft laboratories.

In July of 1973, Mr. Harry E. Pike retired from his position as Business Officer of the Station after 15 years of outstanding service. He was replaced by Mr. John R. McCombs, who earlier had joined the Station staff in December, 1968. Also in July, 1973, Dr. David D. Cudaback was appointed to the newly created position of Associate Director for Astronomy of the White Mountain Research Station. The establishment of this position is a recognition of the important future role the Station facilities are expected to play in support of astronomical research.

Finally, in the summer of 1973 the U. S. Navy transferred title of all their buildings and equipment at the Station to the University of California. At the same time, negotiations between the University and the U. S. Forest Service were initiated by Mr. J. Roger Samuelsen, Coordinator of Special Projects, Office of the Vice President—University Relations, and Mr. Everett Towle, Forest Supervisor, Inyo National Forest, to implement appropriate special use permits for continued operation of the Station by the University.

$3 million operation

In the first 25 years of year-round operation of the White Mountain Research Station, it has grown into a complex of laboratory facilities encompassing an altitudinal range from 4,050 feet in the Owens Valley to 14,250 feet at the summit of White Mountain Peak. Most of the growth has been made possible by the acquisition of government surplus military materiel through the Office of Naval Research (ONR). From the beginning, Mr. Elmer G. Keith, Resident Representative of ONR on the Berkeley campus, has played a major role in providing this all-important resource.

The value of the physical plant can be set conservatively at $3 million; but the fundamental scientific importance of the unique combination of location, environmental characteristics, and laboratories is inestimable. Above all, the dedicated spirit of the Station staff, their accumulated operational experience in this harsh and unforgiving high-mountain environment, together with their specialized logistic support equipment, would be very difficult to duplicate.

Perhaps the best gauge of the worth of the White Mountain Research Station is the record of teaching and research activities reflected in the theses and publications that have emanated from the work performed there. A list, probably not complete, of more than 350 technical papers published during the 25 years of the Station's existence appears as an appendix to this document. It should be noted that the list includes the dissertations submitted by 23 successful Ph.D. candidates, one successful D. Eng. candidate, and 10 successful M.A. candidates, all of whom utilized the Station facilities for their thesis research. In the sections that follow, an appraisal is made of the research results represented by these 350 publications.

White Mountain is truly an institution of highest learning.

THE MEN OF VISION AND FAITH

It is frequently forgotten that a scientific enterprise cannot exist without financial and administrative support, and that the basic decisions to provide such support are not usually made by the scientists who participate directly in the enterprise. The historical record of the White Mountain Research Station would not be complete without the grateful acknowledgment of the many individuals who assumed responsibility and actively supported its development and operation over the years. It is not possible to list them all, but particular mention must be made of those whose names follow.

Of The University of California

Chancellor Albert H. Bowker
Vice Chancellor Mark N. Christensen
Dean Sanford S. Elberg
Assistant Vice President Loren M. Furtado
Chancellor Roger W. Heyns
President Charles J. Hitch
Vice Chancellor Robert F. Kerley
President Clark Kerr
Regent John H. Lawrence
Assistant Chancellor Errol W. Mauchlan
Regent Donald H. McLaughlin
Assistant Business and Finance Officer Frank W. Miller, Jr.
Chancellor Emil M. Mrak
Chancellor Glenn T. Seaborg
President Robert G. Sproul
Coordinator of Academic Affairs Charles Susskind
Vice President Angus E. Taylor

Of the Supporting Agencies[1]

Dr. Harve J. Carlson, ONR and NSF
Dr. William V. Consolazio, ONR and NSF
Dr. Dale W. Jenkins, NASA
Mr. Elmer G. Keith, ONR
Dr. Louis Levin, ONR and NSF
Dr. Leonard M. Libber, ONR
Dr. Freeman J. Quimby, ONR
Dr. Orr E. Reynolds, ONR and NASA
Dr. Joseph F. Saunders, NASA
Dr. Warren Weaver, Rockefeller Foundation

[1] ONR (Office of Naval Research); NSF (National Science Foundation); NASA (National Aeronautics and Space Administration).

Of the U. S. Forest Service

Forest Supervisor Eldon E. Ball, Inyo National Forest
Forest Supervisor Wilfred S. Davis, Inyo National Forest
White Mountain District Ranger Jonathan F. Hoefer, Inyo National Forest
Forest Supervisor Joseph T. Radel, Inyo National Forest
Forest Supervisor Everett Towle, Inyo National Forest

AVIAN PHYSIOLOGY

Arthur H. Smith[1]

Studies of adaptive changes in colonies of domestic birds maintained at high altitude were planned in 1951. Birds were considered particularly suited to these objectives because of their ovipary, which permits the application of suitably different environments to developing embryos and adults. In addition, other aspects of environmental physiology of the domestic fowl having been extensively investigated for reasons of husbandry, our results from high-altitude studies may be more broadly interpreted than would be otherwise possible.

Our initial studies at White Mountain were conducted with Broad Breasted Bronze turkeys. Because their nutritional requirements are complex, any impairment in the poults' growth rate at high altitude would indicate any special dietary problems. Month-old poults, hatched at sea level, were taken to White Mountain on April 29, 1953, and housed in a quonset building known as the "met hut" above the Crooked Creek Laboratory. In true White Mountain style, a brooder was improvised from an old kerosene-burning egg incubator with an attached wire screen run, 3 x 8 feet. After brooding, birds were moved to an outdoor pen which contained a crude shelter constructed from prefabricated hut floor segments. Growth rates were found to exceed those ordinarily obtained at sea level (Smith, Wilson, and Pace, 1954; 1955)[2]—indicating that no special nutritional or other husbandry problems existed for domestic birds, at least at 10,500 feet elevation. The principal problem encountered was depredation from the resident felines, a situation which eventually reduced the flock to three birds.

An assortment of adult chickens (Barred Rocks and White Leghorns) were also taken to Crooked Creek on July 12, 1953, and housed outdoors in battery cages. They soon ceased to lay eggs and suffered a 25 per cent mortality in the first four months. The survivors were housed indoors thereafter, in the met hut, and eventually resumed a normal laying rate.

Despite these problems, it seemed quite feasible to maintain chickens at high altitude, and on May 15, 1954, some newly hatched Leghorn chicks were taken to Crooked Creek as parent stock for a colony. The improvised oil-burning brooder, used previously for the poults, was put in working order and the brooding commenced. Unfortunately, it was a short operation. Mice had been nesting in the linters insulation and probably blocked the air circulation. The brooder caught fire during the night, demolishing in succession, the brooder, the chicks, the met hut, and the investigators' morale.

Support for a larger program was secured from the National Heart Institute in December, 1954. The following summer a chicken house (and the shell of an animal building—in atonement for the met hut) was built at the Barcroft Laboratory. Designed by C. F. Kelly, the structure provided 440 square feet of pen space and a separate 200 square feet for brooding (Smith *et al.*, 1959). The builders included undergraduate, graduate, and veterinary students, a high school science teacher, and University faculty. The task was rigorous and equally informative of high-altitude physiology. However, in the tradition of the Mountain, a substantial camaraderie developed; the group called itself the SHCC ("sky-high chicken crew") —a title adopted by subsequent researchers and assistants. The materials used were largely extracommercial—surplus, salvage, and scavenge. Floor slabs were poured during a cold period, and the concrete froze before setting. It was about six months before a match could be scratched on the floor without leaving a furrow. However, the structure proved sound, and for 15 years it has withstood all the mountain had to offer.

Incubation facilities were established at the Crooked Creek Laboratory in 1956. Initially these consisted of a 600-egg capacity wooden incubator, located in a storage building. In 1961, a 760-foot square building was built and equipped with two Jamesway 252 incubators. It also contained space for working with eggs, and a separate room for brooding chicks and holding some adult birds for short-term experimentation. In 1966, additional incubation facilities, including another pair of Jamesway 252's, were established at the Barcroft Laboratory (12,500 feet elevation).

Reproduction

Daily egg production was recorded only on a pen basis until 1963, when the hens were put into individual laying cages for the summer months. For the first three generations, egg production capacity was low—between 30 and 40 per cent (eggs/100 hens/day). Since the fifth generation, with all reproduction at high altitude, it has remained at approximately 50 per cent; however, when hens are transferred from White Mountain to sea level, the laying rate increases to 70 per cent, a respectable commercial rate. Eggs laid at high altitude are somewhat smaller than those laid at sea level, averaging 55.2 gm. The disparity in size appears to result from some metabolic limitation, since hens raised at high altitude lay normal-sized eggs (59.5 gm) upon transfer to sea level. The relative

[1] Arthur H. Smith is Professor of Animal Physiology, University of California, Davis.

[2] See "A Record of Publications . . . Concerning Work at White Mountain Research Station . . ." on page 47 for publications referred to in the text by author and date.

size of the major components—shell, albumen, and yolk—are similar between eggs produced at high altitude and those laid at sea level.

As long as the birds were pen-raised, male fertility —as indicated by the egg fertility—was quite high, generally 90 to 95 per cent. When hens were placed in individual laying cages, and inseminated artificially, fertility decreased to 80 to 90 per cent. However, this change was considered to have a technical, rather than a physiological basis.

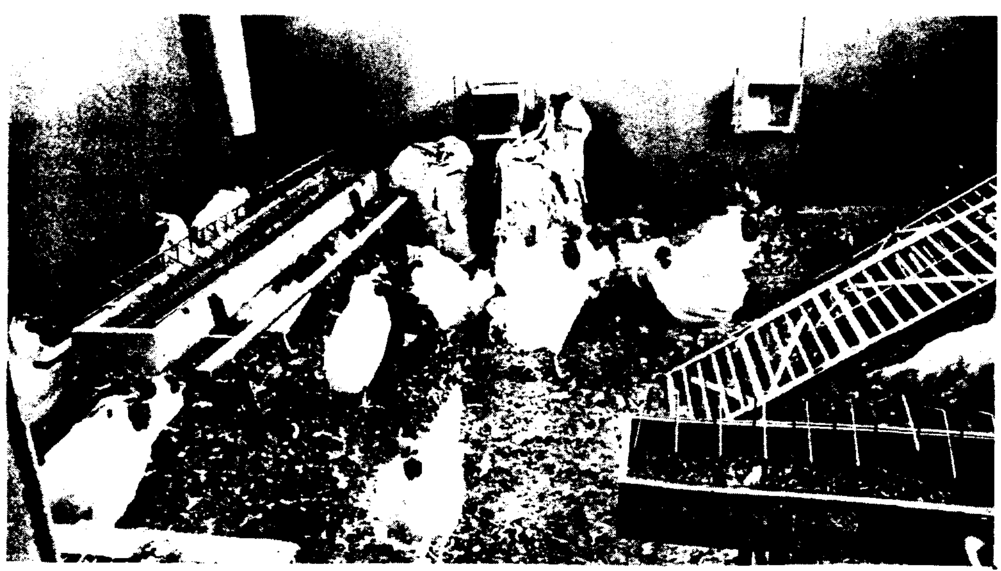
Starting in 1956, eggs were incubated at the Crooked Creek Laboratory (10,150 feet elevation) in wooden incubators; in this environment, only 3 to 5 per cent of fertile eggs hatched. By contrast, the commercial 2,000-egg capacity incubators used after 1961 yielded a hatchability rate of 15 to 20 per cent for sea level eggs comparable to those of the colony's parent stock. At the Barcroft Laboratory (12,500 feet elevation) these commercial-type incubators produced hatchabilities that were 20 to 50 per cent of that obtained with equivalent eggs at 10,150 feet.

With succeeding generations of the high-altitude colony, hatchability (vigorous chicks per 100 fertile eggs) improved considerably over the 16 per cent obtained from the parent stock. The kinetics (hyperbolic) of this improvement indicated a maximum hatchability of 60 per cent for eggs of this strain incubated at 10,000 feet elevation. The change occurred rather rapidly with 90 per cent of the increased hatchability being obtained in the first six generations.

Embryo mortality at high altitude tends to be distributed throughout the three-week incubation period. This is quite different from the usual situation in which embryonic deaths are restricted to the first and third weeks of incubation. Other treatments that depress hatchability also exert their effects during early and late embryonic stages. It is generally conceded that mid-incubation deaths, when they are encountered, result from metabolic derangements. Embryo mortality for the White Mountain line was reduced with succeeding selections, but not proportionately at all developmental stages. The greatest effects were on early deaths (up to seven days incubation) and on the intermediate embryo deaths (7 to 18 days incubation). This improvement was quite rapid, most of it appearing to occur in the first two generations. The reduction of "dead in shell" mortality was exponential throughout—a decrease of 6 per cent (relative to the initial mortality) per selection. Mortality occurring after the start of the hatching process ("pips" and "crippled or died") was not particularly affected by the selection and remained at 5 to 6 per cent of fertile eggs throughout.

Incubation at high altitude not only decreases hatchability but also delays the time of hatching (Smith and Abbott, 1961). With the hatching of pedigreed eggs after the eighth generation, it became evident that the degree of both effects was proportional. A comparison of mean hatching times and hatchabilities on a hen basis, indicated that the maximum hatchability is obtained where hatching occurs after 495 hours incubation (20.6 days)—and that hatchability decreases about 8 per cent with each hour's prolongation of hatching time.

The results of high-altitude selection upon the respiration of chick embryos, which have been partially reported, was investigated in 1963–1964 in collaboration with Dr. John Beattie of Queens' College, Cambridge (Beattie, 1964). When incubated at sea level, embryos of the high-altitude strain had a significantly lesser respiratory intensity than those of sea-level lines. However, at 10,150-feet elevation, respiration of "sea-level" embryos is reduced about 30 per cent, whereas that of the "high-altitude" line is reduced only 10 per cent. After high-altitude hatching, the respiration of chicks of sea-level stocks remains about 18 per cent less than those produced at sea level —but the respiration of the newly hatched chick of the



Right: Professor Arthur H. Smith's experimental poultry colony. Barcroft Laboratory. October, 1957.

White Mountain line is about 2 per cent greater at high altitude than at sea level. Consequently, high altitude adaptation (selection) leads to rather marked changes in the respiratory metabolism of the embryo.

High-altitude incubation also greatly slows the rate of embryogenesis—but with adaptation this returns towards normal kinetics. Growth of brain and heart are particularly affected by hypoxia—the brain never attaining a normal relative size and showing considerably delayed rate of maturation at 3,800 m (Atherton and Timiras, 1971) and the heart showing hypertrophic changes in the last week of incubation (Smith, Burton, and Besch, 1969). However, the onset of polycythemia and of selective right heart hypertrophy appear to coincide more closely with hatching (Burton and Smith, 1969). The influence of hypoxia upon erythropoiesis in the five- to nine-day chick embryo (when hemoglobin synthesis shifts from the fetal to the adult form) also was examined by Atherton and Timiras (1970).

Chronic altitude sickness

Posthatching mortality at high altitude is biphasic. One mortality component has a high rate, 2 to 3 per cent per day, and is restricted to the young—becoming unimportant after 100 days of age. The other component has a lesser rate, 0.07 to 0.10 per cent per day, but persists throughout the residence at high altitude. Over several generations of selection, the first rate component became substantially reduced—to half or less of the initial value. The later mortality component was much less affected with retention of the colony at high altitude—being reduced only 20 to 30 per cent. This mortality is generally preceded by a debilitated condition that is commonly called chronic altitude sickness. Affected individuals generally have a cyanosis of the comb and wattles, and become progressively listless and emaciated. Although the incidence of such debility is less in selected (native) populations, it is qualitatively similar to that developing in newly introduced populations. Its occurrence also is sporadic—so that individuals who have physiologically adapted to and tolerated hypoxia for long periods, may lose that condition, much like the development of Monge's disease among high-altitude human populations.

Below: Lloyd M. Harwood, Farm Adviser, U. C. Agricultural Extension Service, Santa Rosa, and Professor Arthur H. Smith, U. C. Davis, packing eggs laid at the Barcroft Laboratory for shipment to Davis for studies of hatchability at sea level. October, 1957.

Examination of chickens affected by chronic altitude sickness indicates the presence of endocardial lesions (myxoid degeneration), enlarged right heart, and a degenerative emphysema of the lung (Olander, Burton, and Adler, 1967). Comparisons were made of right heart sizes in birds at high altitude, and some at sea level in which an equivalent polycythemia had been induced by androgen. These indicated that chronic hypoxia (independent of polycythemia) induced a right heart hypertrophy (Burton and Smith, 1967). Further examination by Burton, Besch, and Smith (1968) indicated that this right heart enlargement was proportional to the pulmonary arterial pressure. For each 1 mm Hg increase in pulmonary arterial pressure —above the normal 10 mm Hg—there is an increase of 41 mg in right heart mass. This degree of hypertrophic response is much greater than that found in those mammals which develop pulmonary arterial hypertension at high altitude.

Hematology

In chickens maintained at high altitude, the hematocrit value (per cent PCV) increases much as with other species, but with no change in hemoglobin characteristics (Thrasher, 1968). However, in chickens the influence of sex hormones is particularly important —androgens enhancing and estrogens repressing the hematocrit value. This effect of these hormones is quite independent of hypoxic mechanisms (Smith, Ogasawara, and Winget, 1966), and is dominant. Estrogenized hens at high altitude (12,500 feet) exhibit a progressively decreasing hematocrit value, and at 10 per cent PCV, they die. This property has been particularly useful in identifying altitude effects—since sea-level controls can be arranged with similar hematocrit values and *vice versa* (Burton and Smith, 1967; Burton, Besch, and Smith, 1968; Burton, *et al.*, 1969).

The role of the hematocrit value in physiological adaptation to hypoxia has been regarded with skepticism. However, it appears that (in conjunction with other factors) it greatly enhances the retention of consciousness under acute hypoxia (Burton *et al.*, 1969). Also, extremes (high or low PCV) limit exercise capacity at altitude.[3] With low hematocrits, respiratory function becomes insufficient; with high hematocrits, circulatory function may be impaired.

[3] Morse, J. T., unpublished.

At high altitude, there are increases in blood volume—although plasma volume is reduced, and this is not related to changes in hematocrit. However, there are no marked changes in plasma characteristics (Burton, 1965; Burton, Besch, and Smith, 1966). The blood volume of the lung is even more greatly reduced—both relative to lung mass and to body blood volume.

Respiration

Blood gas tensions (CO_2 and O_2) are greatly reduced at high altitude—as would be expected (Burton, Besch, and Smith, 1968). However, the influence of anaesthetics (e.g., pentobarbital) upon blood gas content is considerably different at high altitude and at sea level. At sea level, such anaesthesia reduces arterial oxygen tension about 50 per cent—but at 12,500 feet, the reduction is only 19 per cent.

The avian respiratory system is particularly well suited to studies of oxygen transfer capacity. By inserting an air stream into the trachea, and permitting the gas to exit through an incision in an air sac, a bird can be properly oxygenated, and respiratory movements abolished.[4] In this way a respiratory steady state can be maintained, a condition not possible in mammals. By changing the PO_2 in the perfusing gas and measuring changes induced in the arterial blood, the transfer characteristics of the lung can be determined. This was done at high altitudes (10,000 and 12,500 feet) and at sea level (Besch, Burton, and Smith, 1971). The principal effect of high-altitude exposure is a reduction in the oxygen transfer rate—with little effect on the efficiency of removal of oxygen from the lung gas. With physiological adaptation, both the rate of pulmonary oxygen transfer and the efficiency of oxygen removal from lung gas become enhanced.

Summary

Our experience at White Mountain in raising colonies of domestic birds over several generations has shown that progressive physiological changes occur at various developmental levels. Studies of embryogenesis at high altitude are particularly appropriate with birds inasmuch as the embryos are readily accessible, and their physiology is not complicated by the influence of maternal systems—as in viviparous species. Cardiorespiratory studies also may be profitably explored with avian subjects. Although homeotherms are functionally similar, anatomic arrangements of birds permit several experimental preparations that are not possible with mammals.

[4] Burger, R. E., and F. W. Lorenz. Artificial respiration in birds by unidirectional airflow. Poultry Sci., 39: 236–37, 1960.

Right: Himalayan snow partridge. A breeding pair of these birds was maintained at the Crooked Creek Laboratory in 1966–67. They are natives of the alpine regions of the Himalayas.

STUDIES OF NATIVE MAMMALS

Raymond J. Hock[1]

When I became resident scientist at the White Mountain Research Station, my first inclination to study the physiological mechanisms by which wild native mammals respond to environmental stress was stimulated in part by paucity of information on the subject. An initial search of the literature on mammals revealed a startling fact—that local subspecies of the deer mouse (*Peromyscus*) occurred over the largest altitudinal range known for any small mammal subspecies in North America (and probably in the world). Studies by Dunmire (1958, 1960) on reproduction of deer mice from Owens Valley to the Summit indicated that the 4,000- and 7,000-foot populations bred in spring and fall, with a summer hiatus, while the higher elevation mice bred in late spring and summer. This provided a convenient "calendar" on which to impose sequential studies at various altitudes at the same biological time.

Investigations of hematological parameters and body and organ weights of mice at three sites—Owens Valley, Barcroft, and Summit showed a direct relationship between increases in red blood cell count, hematocrit, and hemoglobin and increased altitude (Hock, 1964). Later study of seven altitudes from sea level to 14,246 feet (sea level, Saline Valley, Westgard, Crooked Creek) confirmed these findings (Hock, 1966).

In subsequent research, mice from the sea-level colony (derived from Salton Sea stock) were translocated to 12,500 feet, and the nature, rate, and extent of the process of acclimatization to high altitude was studied in these mice over a 90-day period. This research represented the beginning of an attempt to distinguish acclimatizing (individual responses to altitude) from adaptive responses (those that are genetically fixed). The sea-level mice translocated to high altitude showed a rapid increase in red cell count and hematocrit to maximal values approximating the high altitude native mice in about 20 days; hemoglobin response was much slower. In about 30 days after return to sea level (de-acclimatization) all three of these blood parameters returned to control values (Hock, 1966).

When high-altitude natives were translocated to sea level (acclimatization to low altitude) for 90 days, red cell number remained the same as high altitude control levels, whereas hematocrit fell to sea-level control values, and hemoglobin was slightly decreased. We may infer from these findings that red cell number is genetically fixed in high-altitude mice, or, alternatively, that there was no stimulus for red cell destruction. Plasma volume increase would account for the decreased hematocrit, and the very slight decrease in hemoglobin can be attributed to experimental variation (Hock, 1966).

Sawin (1969) examined the oxygen-carrying function of the blood of deer mice in relation to altitude and hypoxia. Arterial blood saturation of Barcroft mice was approximately half of that of sea level mice, the oxyhemoglobin curves were shifted to the right, while oxygen transport occurred on the lower portion of the oxyhemoglobin dissociation curve in contrast to its occurrence on the upper portion in the sea-level mice.

Weight studies

In the original altitude survey, body weight was found to increase with increasing altitude (Hock, 1962); however, later examination using a larger number of stations and a much greater number of mice showed that weight plotted against altitude produced a parabolic curve, with the highest weight at 10,150 feet (Hock, 1969). It may be that restriction as a concomitant of exposure to hypoxia reported in rats by Timiras *et al.* (1957) is effective in deer mice above 10,000 feet.

Organ weight/body weight ratios were also studied and demonstrated a clear progression with increasing altitude in terms of heart weight/body weight, with animals at highest elevations showing a ratio 1½ times that of the 4,000-foot animals. The absolute and relative weights of the adrenal glands decreased with altitude in these animals in contrast to rats translocated to high altitude in which adrenal weight and ratio increased rapidly, remaining elevated even in the second generation born at altitude (Timiras *et al.*, 1957). This response in deer mice is clearly opposite to that found in rats, and appears to be of a true adaptive physiological character. Unfortunately, later studies did not give such clear-cut results; consequently, further analyses must be made.

In the deer mice translocated from sea level to Barcroft, relative heart weight did not change during the exposure period, although it was much lower than that of high altitude native mice. Absolute and relative adrenal weights decreased with time at altitude and, again, were lower than those of native mice. After 100 days at altitude, the surviving mice were returned to sea level, and both absolute and relative adrenal weights were seen to increase over the 50 days of study. Spleen weights decreased and lung weights increased at altitude, in each case indicating circulatory and respiratory adjustments that were taking place (Hock, 1969).

The high-altitude natives translocated to sea level (acclimatization to low altitude) showed a decrease in relative heart weight in 90 days, maintenance of the

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relative adrenal weight at high altitude control levels, increase in spleen weight, and maintenance of lung weight. These animals gained weight after translocation, but the relative organ weight changes cannot be explained away by this simple cause (Hock, 1970).

Metabolic rate studies

Metabolic rate studies were made on deer mice by Cook and Hannon (1954) early in the history of the Station. They found that the metabolic rate was lower in Barcroft native mice than in mice from sea level or 4,000 feet, and postulated that such a difference might be due to genetic factors, pelage insulation differences, or tissue hypoxia in the mountain mice. Murie (1960, 1961) confirmed the lower metabolic rate of Barcroft mice, but could find no difference in pelage insulation. He believed that there was no advantage to be derived for *Peromyscus* from the maintenance of tissue hypoxia, and ascribed the metabolic difference found to differences in "nervous temperament."

The most interesting of my own metabolic studies, which differed from those above because they were conducted at the altitude to which the mice were native, was a comparison of oxygen consumption at ambient temperatures from near 0° to 37°C. In summer, sea-level mice had the highest metabolism, mice from 4,000 feet were intermediate, and those native to 12,500 feet were lowest. Mice from the hot Owens Valley easily tolerated the highest temperature which, for the high-altitude mice chronically exposed to a naturally cold environment, proved to be lethal. The high-altitude mice, on the other hand, tolerated 0°C well, whereas the Valley mice became hypothermic at this ambient temperature (Hock, 1962, 1965; Hock and Roberts, 1966).

In fall, metabolic rate studies were made over a smaller range of temperatures—from 20° to 32°C. Both sea-level and high-altitude mice showed the same values for metabolic rate. Small mammals often show a decrease in metabolic rate with the onset of winter, partly due to the increase in pelage insulation. It has also been thought that physiological insulation increased, consisting of decrease in peripheral and central temperatures that acts to decrease heat flow from the body to the environment by reducing the temperature gradient between them. Evidence for the occurrence of this reduced gradient due to the decrease of body or peripheral temperature had not been established for mammals as small as deer mice. In the studies under discussion, deep colonic temperature in the summer series was much higher for the valley mice than for the high-altitude population, while the sea-level mice had temperatures near those of the "high" mice. In February, the mean colonic temperatures for sea-level and Owens Valley populations had shifted downward about 1°C; in short, the mice had increased physiological insulation by decreasing the temperature gradient from the core of the body to the surrounding air, and thus effectively reduced heat loss. The high-altitude mice showed no such seasonal decrease, and their colonic temperatures remained the same. These studies of temperature change were all made with wild-trapped *Peromyscus*, so there is no question of differences due to breeding in captivity.

When metabolic rate response to varying ambient temperatures was determined in February, it was found that the shifting of curves for the various populations seen in fall had progressed, with the high altitude group having the highest oxygen consumption and the sea level population now lowest—a direct re-

Right: Native deer mouse being tested for its exercise capacity on a treadmill at the Barcroft Laboratory. Summer, 1963.

versal of the summer picture. This whole complex of metabolic and temperature changes was interpreted as follows:

Summer metabolic rates

In summer, there is a direct relationship between metabolic rate and the partial pressure of oxygen in the various altitude populations at all ambient temperatures. The low metabolic expenditure of the high-altitude mice in summer appears to approach a minimal level consistent with tissue oxygen demands. This high-altitude summer metabolic rate was lower than that found for sea-level mice at their lowest annual level, indicating the effect of hypoxia on metabolism. Therefore, the high-altitude mice cannot reduce metabolic rate still further in winter, as is common in small mammals exposed to seasonal cold, for to do so would result in tissue hypoxia, and continued existence would be impossible. Because the small size of the mouse prohibits adding pelage insulation in quantities adequate to effectively reduce heat loss and thereby allow decreased metabolic rate, the mouse is forced to increase metabolism and, consequently, body temperature does not decrease.

The sea-level mouse, on the other hand, has a high metabolic rate in summer, coupled with high body temperature. This mouse is not naturally exposed to the extremely low temperatures found at high altitude, and a small increase in pelage insulation accompanied by decrease in body temperature retards heat loss sufficiently to accomplish the reduction of metabolic rate (Hock and Roberts, 1966).

Exercise is a necessary factor in the life of any wild mammal, but vigorous and prolonged exertion is probably never demanded of deer mice. Nevertheless, in order to impose maximal stress, an exercise test was developed for these animals. In an initial study (1960, 1961), I found that mice native to 4,000 feet had mean endurance time of 15.8 minutes, about twice that for the mice at Barcroft. A second study yielded mean times of 16.7 and 11.2 minutes, respectively (1964, 1965). These latter mice were then translocated to the opposite altitude in an attempt to determine whether the observed differences were due to hypoxia or other extrinsic environmental factors, or to some intrinsic factor in the mouse, such as body size, pelage insulation, or the like. The low-altitude mice on translocation were, of course, exposed to the hypoxia of high altitude, and endurance time was found to decrease precipitously on initial transfer and to increase slowly over the 90 days of exposure and acclimatization to altitude. Translocation of high-altitude mice to 4,000 feet could be expected to increase endurance time once removed from the hypoxic inhibition; however, endurance time continued to decrease over the period of exposure and, at the end of 90 days, was about half the high-altitude control value. These findings indicate that some intrinsic factor, not released by the removal of the hypoxic suppression, is operating in these animals. Cardiac anomalies are known to be present in the Barcroft deer mice (Baird and Cook, 1964), and these, in addition to other pathologies, may be coupled with seasonal fluctuations to explain the observed deterioration in performance. Baird and Cook (1964) found cardiac and circulatory anomalies in 87 per cent of deer mice from Barcroft and an absence of such congenital defects in Owens Valley or Salton Sea mice. They ascribed this difference to prenatal hypoxic influences, accentuated by postnatal hypoxic exposure.

Oxygen studies

A third study (Hock, 1965) involved a comparison of sea-level mice translocated to high altitude and native-altitude animals. Exercise oxygen consumption of the sea-level mice did not show increase at high altitude compared to sea level, and high-altitude natives had higher oxygen cost of exercise at both altitudes. In short, the high-altitude mice were less efficient in the total or net oxygen cost of exercise at either altitude.

With the help of Dr. Robert Em. Smith and Ms. Jane Roberts, attempts were made to correlate whole-body metabolic responses of the deer mice with tissue respiration, subcellular and enzyme responses. The metabolic picture has been described above. These studies were made at Barcroft Laboratory with wild-caught native mice, and at UCLA with the sea-level colony mice derived from Salton Sea parentage. All mice were similarly housed and fed.

In the summer series, marked differences were found in levels of liver mitochondrial activity and in several enzyme systems between the two altitude groups. Seasonal studies in both high-altitude and sea-level mice showed changes that were similar in direction to the altitude comparisons. Further studies in sea-level mice exposed to experimental cold tended to show the same response patterns. A comparison of the mean July temperatures of the high altitude site showed it to be identical with the experimental cold exposure at sea level. Consequently, the simple comparative differences we had hoped to find in the two altitude populations were obscured by seasonal and temperature-induced changes (Roberts, Hock, and Smith, 1966).

Brown fat

A more definitive study was that of the brown fat response to altitude. Smith and Roberts had conducted a series of experiments investigating the thermogenic role of this tissue in rodents exposed acutely and chronically to cold, and found that on initial exposure to cold, body temperature and shivering were decreased and metabolic rate increased. Later, increases in both the mass and the metabolic activity of brown fat resulted in a five- to eight-fold increase in the heat production of this tissue. Sea-level deer mice translocated to high altitude showed an increase in metabolic rate, decrease in colonic temperature, and increase in the brown fat mass (Hock, Roberts, and Smith, 1965). Cold exposure studies of the sea-level mice showed an increased estimated heat production of brown fat of about 700 per cent in six weeks. Since the deer mice native to high altitude showed enzymatic changes similar to those found in sea-level cold-exposed deer mice, we further investigated the brown fat response of sea-level deer mice translocated to high altitude. The respective animal rooms involved were kept uniform as to temperature, light cycle, and condition of caging and care, so that any differences found could be ascribed to hypoxia. We also investigated the mass, oxygen uptake of the brown fat homogenate, and the estimated heat production of brown fat of mice native to sea level, 4,000 feet, and 12,500 feet. Translocation of mice in both directions between sea level and 12,500 feet was made to enable us to check metabolic rate, body temperature, and brown fat changes on translocation.

Inspection of the brown fat responses of mice native to the three altitudes was complicated by the fact that the sea-level mice were from a colony maintained at a constant high temperature, whereas the other two populations were of wild-living mice exposed to diurnal and seasonal temperature fluctuations, including cold. Comparisons with cold-exposed sea-level mice did not indicate clear-cut differences between the effects of cold and those of hypoxia.

The translocation to high altitude, with the effects described above occurring at four days of exposure to the hypoxia of high altitude uncomplicated by cold exposure, indicated that body cooling, whether induced by cold exposure or hypoxia, acts to cause increase of brown fat mass. However, because of a depression in brown fat respiration, total brown fat heat production decreased (Roberts, Hock, and Smith, 1969).

When high-altitude native deer mice were translocated to sea level, brown fat mass and respiration increased, so that estimated heat production was similar to that of sea-level cold-acclimated mice. Inasmuch as the translocation did not involve any change in ambient temperature, the brown fat differences observed may be viewed as the result of release from a hypoxic suppression of brown fat respiration imposed both on mice native to high altitude and translocated sea-level mice. Thus the high-altitude natives exhibit cold adaptive responses of both brown fat mass and respiration, but hypoxia may limit brown fat heat production (Roberts, Hock, and Smith, 1969).

Hibernators

Of the numerous other species of mammals on White Mountain—14 species are listed above 12,000 feet (Hock, 1963)—studies have been made on only two, both hibernators: the golden-mantled ground squirrel, *Citellus lateralis*, and the yellow-bellied marmot, *Marmota flaviventris*, Smith and Hock (1963*a*, *b*) described the thermogenic role of brown fat in the arousal of the marmot from hibernation. Despite the existence of such inquiries from as early as 1550, this was the first clear indication of the function in hibernators of this so-called "hibernating gland."

Bullard, Broumand, and Meyer (1966) compared hypoxic effects on rats and ground squirrels, and stated that the ground squirrel is more tolerant even than white rats born and reared at Barcroft. Although hibernators may tolerate hypoxia well, their evidence suggested that the ground squirrel is acclimatized to chronic hypoxia rather than to hibernation.

Blood parameters were also studied by Bullard and Kollias (1966) on summer (nonhibernating) marmots and ground squirrels. Little response was observed to altitude hypoxia in terms of red cell number, hematocrit, or hemoglobin, but greater plasma volume and a shift of the Hb-O_2 dissociation curves to the left was present in both species. I extended the blood studies into fall and winter, including hibernation; polycythemia, increased hematocrit and hemoglobin, were found when compared to summer values (Hock, 1967). Thus, hypoxic "normal" responses appear to occur more in winter than in summer. Consequently, hibernation overrides hypoxia as the factor controlling these blood levels.

Thermoregulatory variations were also studied in these hibernators and compared with hibernating species at low altitude (Hock, 1969). No essential differences in metabolic rate and other thermoregulatory functions could be distinguished between these groups; thus, such responses would appear not to be modified by chronic hypoxia, but by hibernation.

* * * * * * * *

I should like to add a personal note. My years at White Mountain were demanding, but rewarding and stimulating. This is in large part due to the problems and research briefly outlined above. Additionally, it is the result of the associations made there, and the enjoyable camaraderie. Not least is it due to Nello Pace, who in the final analysis made the entire concept, operation, and spirit of the White Mountain Research Station possible. Thank you, Nello.

CARDIORESPIRATORY PHYSIOLOGY

Ralph H. Kellogg[1]

Cardiorespiratory studies at the White Mountain Research Station have been concerned primarily either with the respiratory pigments of the blood and muscle cells, or they have been concerned with the performance of the whole organism, usually man, and the responsible mechanisms at the organ-system level.

The first study, falling into the former category, was carried out by Burton E. Vaughan, one of Dr. Pace's graduate students, who had helped build the Barcroft Laboratory where he did his research. He clearly established that the myoglobin content of the muscles of rats kept at high altitude was significantly increased over that of rats kept at sea level as controls (Vaughan and Pace, 1955, 1956), and he made this the subject of the first Ph.D. dissertation in the biological sciences to come from the White Mountain Research Station (Vaughan, 1955).

At about the same time, Dr. George Feigen and his associates from Stanford University started to use the Barcroft Laboratory, eventually publishing a major statistical study of the blood and plasma volumes and heart weights of rats during acclimatization, studying both male and female, two strains, at various ages (Johnson and Feigen, 1962; Feigen and Johnson, 1964).

During the spring of 1955, when Vaughan's work was first reported, Dr. Pace was organizing a group of physiologists and students for the first study at White Mountain of the second sort, human cardiorespiratory responses and performance during acclimatization. He invited me to spend my vacation as "physician in residence" on the mountain. Although no longer qualified as a physician, I went along anyway and soon became so excited by the unusual opportunities offered by White Mountain that I gradually dropped renal physiology to devote myself to altitude problems.

In addition, the group included Dr. Burton E. Vaughan and several graduate students: E. R. Archibald, Frederick L. Hencken, Ralph Karler, and Thomas I. Koike, plus supporting personnel in Berkeley. The plan was to make three trips to the Barcroft Laboratory for one to two weeks each, separated by deacclimatization periods in Berkeley, when sea level control studies could be repeated. As might be expected, the first trip was plagued by a series of mishaps, not the least of which was that the special gas mixtures were delivered by the supplier to Big Pine Camp, California, instead of Big Pine, California. By the second and third trips, however, good data were obtained concerning the time course of adjustment of the respiratory response to graded inhalation of CO_2 (Kellogg *et al.*, 1956, 1957), the effects of exercise and the reduction in work capacity (Kellogg, 1964), and hormonal changes induced by the altitude stress (Timiras, Pace, and Hwang, 1957).

Celebration at the Summit

That same summer of 1955, the summit road and the shell of the summit building were under construction and both Dr. Pace and I were eager to use them. Beginning in June 1956, we worked hard with Mr. Roche and Mr. Fyfe from the Station staff to convert the summit building into a usable laboratory and living space. For instance, one whole day was required to haul the generator trailer up the summit road with the bulldozer and to seat it in the rocks of the summit. Water tanks, sink, stove, refrigerator, and (with the help of Mr. Robertson of Bishop) the wiring were then installed. Mr. Manis installed a short-wave radio. Finally, the building was ready, and Dr. Pace, Mr. Roche, and I sat down to a sumptuous mountain dinner to inaugurate the inhabitation of the Summit Laboratory.

Unfortunately, just as the Summit was ready for business, Dr. Pace had to return to Berkeley because of the pressure of other duties, However, from his Office of Naval Research funds he generously supported my studies on the Summit for four summers. To replace Dr. Pace, Dr. Vaughan returned to help me. For the first time, human subjects (Berkeley students Donald W. Badger and William Joseph Daily) were flown to White Mountain. Bob Symons of Bishop landed them in his Piper Cub on the meadow by the gate, and they were rushed up the summit road for study, followed two weeks later by two more graduate students, Donal J. Reed and Jack Wohlwill. These 1956 experiments not only defined the time course of ventilatory acclimatization from a more precise initial time but also outlined the course of deacclimatization after the subjects were flown back to Berkeley. The studies demonstrated that the immediate, reversible, ventilatory effect of changing the oxygen pressure during CO_2 stimulation was relatively small compared to the slowly developing but persistent effect of acclimatization (Kellogg, Vaughan, and Badger, 1957; Kellogg, 1963).

Dogs

That same year (1956) Captain E. R. Archibald of the U. S. Air Force, who had been involved in the first CO_2-response measurements at Barcroft in 1955, carried out his Ph.D. dissertation research under Dr. Pace at Barcroft on the CO_2 response of unanesthetized dogs during acclimatization (Archibald, 1964). Also in that year, Dr. J. T. Hansen and others, also working under Dr. Pace, made a few studies of CO_2

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responses at altitude (Gilfillan *et al.,* 1958) in dogs whose carotid and aortic chemoreceptors had been completely removed with the help of a vascular surgeon, Dr. Rutherford S. Gilfillan (Gilfillan *et al.,* 1967). These studies proved to be beyond our technical capabilities at that time, and the problem was set aside until 1968, when Dr. Mines, Dr. Sørensen, and I took it up again using carotid-denervated goats (Mines, 1968). The dogs were found useful, however, by Donald W. Badger, who had been one of the first two subjects on the Summit. He based his Ph.D. dissertation under Dr. Pace on a very extensive study of the plasma and red cell volumes of dogs maintained for months at the Barcroft Laboratory, and, using Hansen and Gilfillan's dogs, he showed that chemoreceptor removal did not interfere with the red cell response to altitude but actually increased it (Badger and Pace, 1962; Badger, 1963). Dr. Hansen, meanwhile, developed a completely automated system for determining cardiac output repeatedly by the dye-dilution principle in awake and undisturbed dogs; he found that at Barcroft, the cardiac output measured under these conditions declined until about the ninth day at altitude, when it stabilized at about 72 per cent of the sea-level value (Hansen, Pace, and Barnstein, 1964).

Joseph K. Gong, another of Dr. Pace's students, followed up Badger's red cell studies by demonstrating that altitude increased the erythropoietic part of the bone marrow of dogs at the expense of the marrow fat without affecting the total amounts of marrow or bone (Gong, 1963*a, b,* 1965).

Sheep

More recently, Drs. Boyer, Crosby, and Noyes of Johns Hopkins, in association with Drs. Kaneko, Keeton, and Zinkl of U. C. Davis, discovered that a sheep which produced primarily hemoglobin A at sea level produced an increased amount of a different molecule, hemoglobin C, after being taken to the White Mountain Research Station (Boyer *et al.,* 1968).

Humans

Let us return now to the chronology of human cardiorespiratory studies at White Mountain. Dr. Pace obtained a National Science Foundation grant to bring Dr. Per-Olof Åstrand and his wife, Dr. Irma R. Åstrand, from the Royal Gymnastic Institute of Stockholm to work at the Station in the summer of 1957. Sharing subjects and facilities with me, they discovered that the heart rate immediately accelerates when oxygen pressure is restored to a subject during severe exercise at 14,250 feet; (Åstrand and Åstrand, 1958*a, b;* 1953). Meanwhile, Donal J. Reed, the late Arthur R. Todd, and I demonstrated that during acclimatization, breathing was stimulated to a given level by abnormally low CO_2 pressures, even while oxygen was being administered to eliminate hypoxia, and while the arterial blood was distinctly more alkaline than normal (Kellogg, Reed, and Todd, 1958; Kellogg, 1963*a, b*). This contradicted the current concept of the mechanism of ventilatory acclimatization and left a question, which was not to be answered until 1962 by Dr. John W. Severinghaus and his associates.

Above: W. Joseph Dailey, medical student, U. C. Berkeley, having his respiratory response to carbon dioxide measured by Assistant Professor Ralph H. Kellogg, U. C. Berkeley, in the first set of experiments at the Summit Laboratory. July, 1956.

Sleep and exercise

That same summer (1957), D. J. Reed began his doctoral research under me on the effect of sleep on breathing at altitude (Reed and Kellogg, 1958).

Above: Fenton C. Kelley, graduate student, U. C. Berkeley, examining a blood sample under the microscope. Summit Laboratory. August, 1958.

He found that sleep depressed breathing (by altering the response to CO_2) sufficiently to make persons significantly more hypoxic (Reed, 1959; Reed and Kellogg, 1959; 1960*a*, *b*). Thus, a person sleeping at 14,250 feet (the Summit Laboratory) became as hypoxic as a person awake at 16,000 feet. This probably explains why persons at altitude commonly wake up with a headache that may go away during the day but reappear the next morning.

In 1959, Dr. S. M. Tenney of Dartmouth led the first of several expeditions to White Mountain. He and his associates have shown that both high CO_2 and low O_2 potentiates gastric secretion of HCl in man (Naitove and Tenney, 1960, 1962), that the alveolar-arterial oxygen gradient in anesthetized dogs is less at altitude, corresponding to only a 4 per cent shunt instead of a 12 per cent shunt (Kreuzer, 1960; Kreuzer *et al.*, 1960), and that the diuresis ordinarily produced by CO_2 inhalation is abolished during the respiratory alkalosis on the first day at 14,250 feet (Valtin and Tenney, 1960; Valtin, Tenney and Larson, 1962). They also have re-studied the interaction of O_2 and CO_2 pressures as respiratory stimulants in man during acclimatization (Tenney, Remmers, and Mithoefer, 1963; 1964).

Above: Sheep at the Crooked Creek Laboratory in red blood cell study by Professor Jiro J. Kaneko, U. C. Davis. Summer, 1963.

The National Science Foundation provided funds which made it possible to invite Dr. Pierre Dejours of Paris to join Dr. Pace and me and our students for the summer of 1960. They demonstrated that acclimatization at the Barcroft Laboratory can change both the quick, neurogenic, and the slow, humoral components of the ventilatory response to exercise (Dejours, Kellogg, and Pace, 1963; Dejours, 1964). The Barcroft treadmill and Tissot gasometer were acquired for this study, and for the first time, a Grass polygraph and other sophisticated electronic equipment were taken up for modern multichannel recording.

The summer of 1962 brought a new group of investigators to the Barcroft Laboratory, led by Dr. John W. Severinghaus of U. C. San Francisco, including Dr. Robert A. Mitchell, a co-discoverer of the medullary chemoreceptors and their role in the ventilatory response to CO_2 inhalation. They thought that the puzzle posed by our findings in 1957 at White Mountain (Kellogg, Reed, and Todd, 1958) might be solved in terms of the newly-discovered medullary mechanism. In courageous experiments involving repeated lumbar punctures on each other to draw samples of their cerebrospinal fluids, they demonstrated that the bicarbonate concentration in cerebrospinal fluid falls so rapidly at altitude (compared to its rate of fall in blood plasma) that the change in CO_2 response in acclimatization can be accounted for by the resulting change in the relation between P_{CO_2} and pH at the medullary chemoreceptors, whose response to pH remains unaltered (Severinghaus *et al.*, 1963; Severinghaus and Mitchell, 1963; Severinghaus *et al.*, 1963*a*, *b*).

This exciting finding was added at the last moment to the program of the International High Altitude Symposium held that summer at Interlaken, Switzerland, in connection with the XXII International Congress of Physiological Sciences, and Dr. Severinghaus's report, delivered just a few days after the experiments had been completed, was the high point of that symposium (Severinghaus and Mitchell, 1964).

Aging and acclimatization

In that same year, Dr. David Bruce Dill of Indiana University and later of Nevada Southern University arranged for a reunion at White Mountain of six of the eight surviving members of the International High

Below: Arseilo P. Carvalho, graduate student, U. C. Berkeley (now Professor at the University of Coimbra, Portugal), and Professor Pierre Dejours, Paris (now Director, Laboratory of Respiratory Physiology, Strasbourg, France), drawing a blood sample for lactate analysis from Professor Nello Pace as he walks on the treadmill at the Barcroft Laboratory. Summer, 1960.

Altitude Expedition that he had led to the Chilean Andes in 1935. Drs. Will H. Forbes, Francis G. Hall, Ancel Keys, Ross A. McFarland, and John H. Talbott were able to join Dr. Dill and his associates. The aim was to repeat their classical studies on the same subjects 27 years later, in order to study the effects of aging on the ability to acclimatize (Dill, 1963*a, b;* Terman, 1963; Dill, Terman, and Hall, 1963; Terman and Newton, 1964; Dill *et al.*, 1964). The presence of Dr. Severinghaus at the Barcroft Laboratory at the same time made it possible for them to cross-check their classical methods with the newest electrical techniques. Dr. Dill has become a major user of White Mountain, leading repeated trips in the subsequent years to study work capacity (Dill *et al.*, 1966, 1967; Klausen *et al.*, 1966), changes in blood and plasma volumes (Dill *et al.*, 1969) and related aspects of acclimatization.

More studies

Dr. Severinghaus, too, has become a major user of White Mountain, returning in 1963 to show that the rapid fall in cerebrospinal fluid bicarbonate in acclimatization does not depend upon a fall in plasma bicarbonate, although it can be accelerated by ingestion of ammonium chloride (Severinghaus, 1964, 1965; Severinghaus, Mitchell, and Singer, 1964). He also measured human cerebral blood flow (Severinghaus *et al.*, 1966), which is increased about 24 per cent during the second six hours at Barcroft but then declines after three to five days to only about 12 per cent above its sea level control value, and he has devoted considerable effort on more than one trip to trying to elucidate the mechanism of the pulmonary edema that sometimes develops at high altitude.

In 1963, Allan H. Mines, a student, I, and others returned to study human pulmonary mechanics during acclimatization (Kellogg *et al.*, 1965), and subsequently returned again with Dr. Søren C. Sørensen of Copenhagen to study the respiratory responses of goats, which, unlike Hansen's dogs, seem to acclimatize satisfactorily after chemoreceptor denervation (Mines and Kellogg, 1968; Mines, 1968).

Probably the first group to use the White Mountain Research Station to study the mechanism of a disease occurring at sea level was that of Dr. A. Dawson of La Jolla, who had noticed a redistribution of blood flow relative to the distribution of ventilation in the lungs of patients whose disease made them hypoxic at sea level. He brought to the Crooked Creek Laboratory the elaborate radioactive counting equipment needed to study this in chronically hypoxic men who were otherwise normal (Dawson and Kahler, 1969).

Another "first" occurred when Dr. Pace and his students took chronically catheterized monkeys to the Barcroft Laboratory (Inge, 1965), probably the first use of non-human primates in a mountain laboratory since Angelo Mosso took some to Monte Rosa for relatively unproductive observations around the turn of the century.

In summary, it seems fair to say that the founding of the White Mountain Research Station, by making it relatively easy for American physiologists to apply the most sophisticated laboratory methods to the cardiorespiratory study of men and animals while acclimatizing to high altitude, has resulted over the past two decades in a reawakening of this field of research. Formerly, altitude acclimatization was considered a rather esoteric subject studied by South Americans in the Andes or, for other physiologists, by mounting elaborate foreign expeditions once or twice in a lifetime; work carried out at White Mountain has not only stimulated new interest in the problems but has raised the standards of work from field methods or intermittent chamber exposures to the best laboratory quality. Moreover, when Dr. Severinghaus and his associates used the change in cerebrospinal fluid bicarbonate in altitude acclimatization to demonstrate the physiological importance of the newly-discovered medullary chemoreceptors, many physiologists came to realize that high altitude could constitute a valuable tool for elucidating mechanisms that are important at sea level, as well as in remote mountains. Whereas 20 years ago, one wondered when a high altitude cardiorespiratory paper would be scheduled in the meetings of the American Physiological Society, there are now usually one or even two sessions devoted to high altitude work, with vigorous discussion by critical investigators working in the field.

ENDOCRINOLOGICAL STUDIES

Herbert H. Srebnik[1]

In support of the early reports of the Spanish conquistadores who settled the Peruvian Andes in the sixteenth century, there is now considerable evidence that growth and skeletal maturation is retarded at high altitude and that infertility and reproductive failure are common afflictions of mountain dwellers. Both growth and reproduction are known to require the presence of hormones secreted by the pituitary gland and some of its target organs, and moreover, the response to stressful environmental conditions—such as the low atmospheric oxygen tension which exists at higher elevations—also is mediated by hormones produced by the adrenal gland.

Not surprisingly then, the establishment of the White Mountain Research Station presented a unique opportunity for the endocrinologist to study the effects of altered environment on hormone-dependent functions of man and lower animals. Initially, efforts were made to collect data on the gravimetric, morphologic and physiologic changes occurring in endocrine organs of animals transferred from sea level to the Station. Later, these studies were extended to cover reproductive capacity and pituitary function of translocated and native high-altitude rats. Most recently, attempts have been made to investigate the relationship between growth retardation and thyroid insufficiency at altitude.

The first published report concerning the endocrinologic status of experimental animals at the Barcroft site (12,500 feet) of the Laboratory appeared in 1956 (Timiras *et al.*, 1956*a*, *b*). A team of Berkeley physiologists led by Dr. P. S. Timiras and Dr. N. Pace reported the results of a comparison made between rats exposed to high altitude for varying periods of time and control animals maintained at sea level but otherwise kept under comparable circumstances. They found that translocation did not immediately affect the weights of the pituitary gland, the testes, or the thyroid. However, even brief exposure to the hypoxic condition (one to three days) elicited the typical stress response, that is, enlargement of the adrenal glands and involution of all lymphoid tissue. These signs were taken as presumptive evidence that the circulating levels of certain adrenal hormones are increased at high altitude.

However, more direct proof for adrenal hyperfunction during early acclimatization was obtained in six human volunteers brought to White Mountain for five to eight days (Timiras, Pace, and Hwang, 1957). Both circulating adrenal hormones and their urinary excretion products rose dramatically over sea level control values, but, predictably, the increase was only transient, diminishing as adaptation to the new environment continued. Other studies in human subjects sojourning for two weeks at Barcroft showed that the urinary excretion of norepinephrine doubled in the course of their stay (Pace, Griswold, and Grunbaum, 1964), suggesting a more prolonged functional response of the sympathetic nervous system to high altitude. In rats whose adrenal glands had been surgically removed, the stress of a 72-hour fast caused much greater mortality at altitude than at sea level (Timiras, 1958).

Growth and reproduction

High-altitude research at Barcroft in the areas of growth and reproduction was initiated by A. A. Krum, a graduate student in the Department of Physiology, U. C. Berkeley. In his doctoral dissertation (Krum, 1957), he concluded that rats brought to the Station from Berkeley could be bred successfully and do deliver normal young. With Timiras *et al.* (1957), he reported that growth of translocated rats (parental stock) ceased earlier than it did in sea level controls and that the second filial generation (F_2), of normal size at birth, soon began to lag behind control rats, both in body weight and dimensions. Interestingly, adrenal hyperfunction was not observed in F_2 rats, suggesting perhaps genetic adaptation to the hypoxic environment. There were no significant changes in pituitary, testes, or thyroid weights in these animals as compared to their sea-level counterparts. The growth rate of these high altitude natives remained subnormal, even when the animals were brought to sea level and kept there for several months (Timiras, Tomsich, and Hwang, 1959).

Wild deer mice

Among the wildlife populating the higher elevations of the White Mountain range, the deer mouse (*Peromyscus maniculatus*) serves as one example of a free-ranging high-altitude native. Growth and reproduction in this species have been investigated in some detail by Dunmire (1958, 1960, 1961) and, somewhat later, by Hock (1962*a*). Dunmire concluded that although the breeding season for deer mice trapped in the vicinity of the Barcroft Station was shorter than that of animals living near sea level, their reproductive function was unimpaired. The onset of sexual maturity occurred at the expected time and, in fact, pregnant mice had bigger litters and fewer resorptions than did those caught at lower elevations. On the premise that the growth retardation resulting from hypoxia might be related to depressed metabolic activity and, by implication, hypothyroidism, Hock compared the meta-

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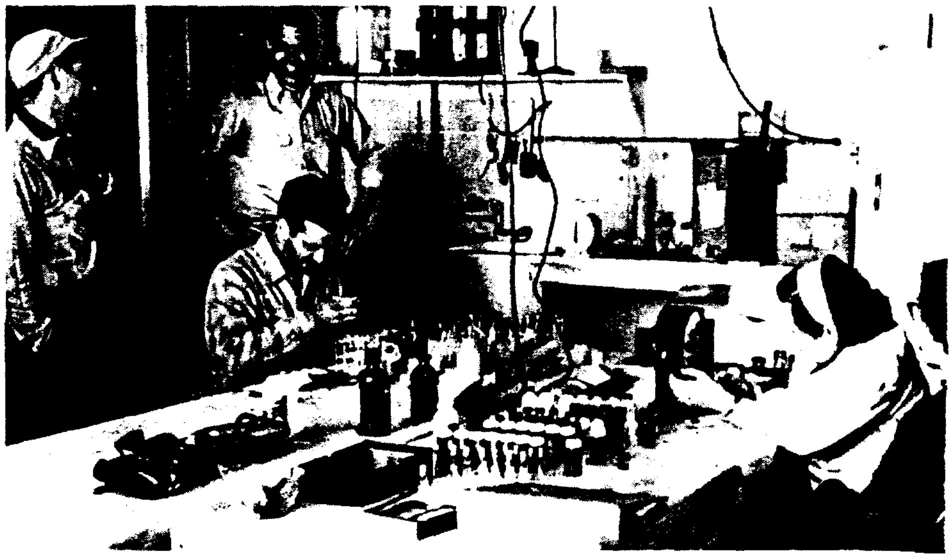
Right: William V. Consolazio, National Science Foundation, and Professor Nello Pace visit the Barcroft Laboratory during an endocrinological experiment by Mr. Peter Miljanich, graduate student, Dr. Paola S. Timiras, and Miss Constance Hwang, technician, U. C. Berkeley. June, 1956.



bolic rates of deer mice at various altitudes (1962*b*, 1965; 1968). The results were highly variable and inconclusive, but seemed to indicate that the metabolic rates of deer mice are influenced not only by oxygen tension of the atmosphere but also by other environmental factors, such as climate (Roberts, Hock, and Smith, 1966). Translocation of high-altitude native deer mice to sea level had no effect on total body weight over the three-month test period (Hock, 1969).

Body/organ studies: laboratory rats

The most recent phase of endocrine research at the White Mountain Research Station was prompted by the studies of Drs. Timiras and Woolley (1966) who measured body and organ weights of Berkeley native stock rats brought to altitude and of their first and second generation offspring. Postnatal body weight was found to be markedly subnormal in F_1 and F_2 progeny irrespective of age and sex, and absolute weights of gonads and sex accessories, e.g., uterus and seminal vesicles, and of pituitary glands were lower in high altitude natives than in sea level controls. Additional work by Dr. Nelson (1969) has since confirmed the interesting observation that term fetuses and newborn rats of females transported from Berkeley to 12,500 feet elevation are indistinguishable at birth from those of sea-level controls with respect to size and endocrine organ weights. Placental weights, however, were greater at altitude, indicating some degree of maternal protection of the fetus at low atmospheric oxygen tension (Petropoulos, 1970, 1972; Petropoulos and Timiras, 1971). The possibility that post-partum changes were due to reduced maternal food intake incidental to loss of appetite at altitude or that they resulted from faulty lactational performance, as proposed by Krum, was examined subsequently by Dr. Nelson and me (1972), but could not be substantiated. Reproductive performance both of translocated Berkeley stock and of high altitude native rats was impaired; however, qualitative differences existed between the two groups, the latter having less regular estrous cycles, fewer fertile matings, and a smaller number of corpora lutea than the parental stock.

From these investigations emerged the tentative conclusion that the hypoxic environment depressed the gonad-stimulating and growth-promoting functions of the pituitary gland. The amount of growth hormone and thyroid-stimulating hormone present in pituitary glands of rats born at high altitude and necessary for normal bone growth and maturation was determined by Nelson, Srebnik, and Timiras (1968) and Nelson (1968) when the animals were 40 days of age. Both of these hormones were significantly reduced in the pituitaries of high-altitude native rats when compared to the content of glands from sea level controls. The morphology of the pituitaries of the experimental animals also differed from that of controls, resembling the early changes seen in pituitaries of hypothyroid rats.

As part of the continuing investigation, thyroid gland activity of rats born and raised at Barcroft Laboratory was assessed by Nelson (1968, 1970) in a variety of tests. The results do, indeed, suggest that thyroid function is adversely affected at high altitude, though it remains to be determined whether this impairment is a direct result of the hypoxic environment or whether it is a manifestation of reduced pituitary thyrotrophic function. If the latter alternative proves to be the correct one, then a thorough examination of the influence of low ambient oxygen tension on the central nervous system is indicated. For the nervous regulation of the pituitary gland is now well established, and it may well be that the disturbances in growth and reproduction which occur at high elevations have a neuro-endocrine basis. In this new venture, we hope to work closely with those of our colleagues who have been directing their efforts to the exploration of brain development and function at high altitude.

NEUROBIOLOGICAL STUDIES

Paola S. Timiras[1]

The nervous system, in general, and especially the higher nervous centers, such as the brain, depend on an adequate supply of oxygen for their normal function. Any interference with oxygenation, whether intrinsic or extrinsic, will impair nervous function, as reflected in morphological, biochemical, and behavioral alterations. While the need for normal circulatory and respiratory exchanges is always crucial to the function of the central nervous system (CNS), during development even transitory periods of moderate hypoxia may irreversibly alter the timetable of CNS maturation. It is generally accepted that the fetus and newborn are more capable than the adult of withstanding short-term exposure to severe hypoxia, but mere survival does not preclude the possibility of delayed maturation and long-term impairment of CNS function.

The White Mountain Research Station provides a useful facility for the systematic study of both short-term and long-term effects of high altitude on the adaptive responses of the CNS in humans and in native and laboratory animals at various stages of growth and development. In general, studies in humans have included investigations of the behavioral correlates of acclimatization and CNS regulation of respiratory responses, particularly in relation to acid-base changes in cerebrospinal fluid. In laboratory animals, mainly rats, our focus has been on the selective effects of hypoxia on specific brain structures, and on the electrophysiological and biochemical maturation of the brain during development. The study of the nature and magnitude of nervous control of adaptive responses is important not only in terms of identifying the mechanisms by which the environment affects the function and development of the nervous system, but also in terms of assessing the ability of the nervous system to respond to environmental extremes.

Human studies

The behavioral symptoms of altitude sickness—deterioration of memory, judgment, and the ability to perform discrete motor tasks—have been extensively described. Other symptoms, equally reflective of subtle changes in CNS physiology consequent to high altitude exposure, are variable and sometimes contradictory; sleepiness, insomnia, lassitude, restlessness, mental fatigue, irritability, and euphoria. As has been observed in human subjects residing at the Barcroft Laboratory for varying periods of time, these behavioral manifestations, although transitory, are sufficient to impair performance. Additional information gathered on these subjects has indicated that temporary exposure to moderately high altitude has deleterious effects on short-term memory (Phillips and Pace, 1966).

The behavioral responses of sea-level inhabitants living temporarily at high altitude have been compared with those of sea-level residents as well as those of high-altitude natives; despite an impressive amount of valuable data that has been amassed on these neurological characteristics, little is yet known of the precise neurophysiological and neurochemical correlates involved in the adaptive responses observed. Studies of electroencephalographic activity, sensory thresholds, and reflex activity have demonstrated that definitive changes occur in these parameters, both during adaptation to high altitude and during subsequent transfer to sea level. Further investigation of these electrophysiological and neurochemical changes is continuing in an effort to elucidate the ways in which the organism generally adapts to changes in environmental oxygen, and to explicate the specific responses of the CNS. In this respect, animal studies are most useful, since they permit identification of isolated phenomena that can then be investigated in depth.

The studies of altitude-induced changes in respiration have been essentially concerned with comparing respiratory responses at different ages, under conditions of rest and exercise, during sleep, and after the administration of barbiturates—drugs known to selectively depress the respiratory centers in the medulla. In all cases, the medullary centers regulating respiration are significantly affected by exposure to high altitude, as described previously in this report, and these effects have been related to changes in ionic metabolism and acid-base balance of the whole organism and, specifically, of the cerebrospinal fluid (Severinghaus *et al.*, 1963, 1966; Severinghaus and Mitchell, 1964; Severinghaus, 1965.

An understanding of the etiopathology of the neurological symptoms attendant to exposure to high altitude is important not only with respect to the health and performance of populations living and sojourning at high altitude, but it is particularly valuable in making extrapolations to other situations characterized by transient or permanent hypoxia. For example, the increasing number and use of non-pressurized airplanes by private individuals raises the potential incidence of accidents due to human failure involving transitory but crucial CNS disturbances. Similarly, as previously mentioned, reduced oxygen at any age may have serious consequences—during early development when organs and systems are undergoing rapid growth, as well as in the elderly in whom the respiratory activity of neural cells is already impaired by progressive alterations in cerebral vessels and by the accumulation of metabolically inert intracellular pigments. Indeed,

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in a very general sense, the aging brain has been viewed as hypoxic, and such comparisons have been tentatively explored in isolated gerontological studies.

Animal studies: adulthood

The maintenance of a permanent rat colony at the Barcroft Laboratory permits a wide variety of carefully controlled, systematic studies to be conducted on a number of aspects of CNS adaptation to high altitude (Timiras, 1965). Our principal continuing interest has been the study of gross brain activity, as measured by electroconvulsive responses, and localized spontaneous and evoked electrical activity as recorded from chronically implanted electrodes in the rhinencephalon, an area including olfactory and limbic structures and actively implicated in a variety of adaptive responses.

We have found that exposure to high altitude induces an increase in seizure susceptibility, as demonstrated by alterations in electroshock seizure responses (Woolley, Herrero, and Timiras, 1963), increased convulsive activity of the spinal cord (Heim and Timiras, 1964), and specific convulsive reactions to neurotropic drugs (Castillo, 1964*a,b*). Deacclimatization is accompanied by CNS depression, similar to that produced by hypercapnia and hyperoxia—a finding that suggests alterations occurring in CNS sensitivity to CO_2 and O_2 (Woolley, Herrero, and Timiras, 1963). The increase observed in convulsibility can be related to changes in brain chemistry, such as increased acetylcholinesterase activity and decreased cortical gamma-aminobutyric acid content in some brain areas—findings that implicate alterations in neurotransmission (Timiras and Woolley, 1966). It has also been noted that recovery time from seizures is longer at high altitude than at sea level, and this differential may be accounted for by the decrease observed in brain glycogen among high altitude animals (Woolley and Timiras, 1963).

The electrical activity in the rhinencephalon appears to be depressed during exposure to high altitude; the amplitude and frequency of spontaneous activity of the prepyriform cortex, olfactory bulb, and hippocampus are all decreased, as is the amplitude, frequency, and number of oscillations of the evoked response in the prepyriform cortex (Woolley and Timiras, 1965; Wing, 1966; Woolley, Barron and Timiras, 1966; Wing, Woolley and Timiras, 1967). In addition, the latency of the evoked response is prolonged in high altitude animals (Williams, Woolley, and Timiras, 1966). The results suggest that the increased seizure susceptibility consequent to exposure to high altitude is a "release" phenomenon that is attendant to the depression of telencephalic centers normally controlling the lower CNS centers.

Throughout the course of these studies in adult animals, it was consistently noted that the maturation of the central nervous system was markedly delayed in animals developing at high altitude. These observations directed us to continue these studies in the developing rat, in which the brain, relatively immature at birth, undergoes accelerated maturation during the first three postnatal weeks. Highly specialized studies have been conducted in the rat brain during this developmental period and have established important data that serve as baseline information for comparative studies.

Animal studies: development

Electrophysiological and biochemical research conducted in developing rats at the White Mountain Research Station has effectively demonstrated that the immature CNS, despite its greater resistance to hypoxia than that of the adult, is nevertheless profoundly affected by changes in environmental oxygen. It appears reasonably certain that any sudden decrease in available oxygen during parturition, at birth, or in the neonatal period, even at sea level, is capable of inducing immediate and often permanent CNS damage, varying in severity depending upon several factors: the degree of hypoxia, the duration of exposure, the stage of development and maturation of the discrete brain structure affected. The differential effects of an oxygen-deficient environment on many aspects of neurological and somatic development have been amply established by continuing intensive studies at high altitude conducted in association with sea-level studies. Our interest in CNS development and CNS/endocrine relationships has emphasized the distinction between the adaptation characteristic of animals born and raised at high altitude for several generations, and the adjustments of an animal placed for short or long-term periods in a hypoxic environment (Timiras and Woolley, 1966; Petropoulos, Vernadakis, and Timiras, 1969). The responses of the neonates born of mothers maintained for several generations at the White Mountain Research Station, though generally retarded with respect to corresponding parameters studied in neonates at sea level, reflect a better accommodation to the environment than the responses observed in the newborn of mothers acutely exposed to altitude. On the other hand, the effects of chronic exposure to high altitude become progressively more severe with each successive generation, and whereas many of the disturbances in growth and development apparent in animals acutely exposed to high altitude are reversible, those in the native population frequently are not. For example, the subnormal body growth typical of animals born at high altitude is difficult to reverse, even long after descent to sea level, and cardiac hypertrophy, characteristic of native stock, persists throughout the lifespan (Timiras, 1964).

Mechanisms of hypoxia effects

The mechanisms underlying the effects of hypoxia on general and specific developmental phenomena have been sought at many levels—from gross considerations of nutritional and maternal factors to complex studies of biochemical and neurophysiological parameters, particularly brain protein synthesis and neurotransmission, both implicated in CNS maturation. Several experiments have conclusively demonstrated that the development of brain excitability is delayed in animals born at high altitude, as shown by a marked retardation in the sequential appearance of convulsive responses with age (Heim and Timiras, 1964). One of the main purposes of our research has been to identify the causes of such alterations in brain electrical activity in hypoxic animals. Thus far, our findings have shown that total DNA content in several brain areas is lower in high altitude animals than in controls, a finding which suggests that the rate of neuronal and/or glial cell proliferation is altered. RNA content, on the other hand, is increased in all brain structures of high altitude animals.

Inasmuch as the CNS is known to respond to increased functional demands by increasing RNA synthesis, the RNA increase observed has been interpreted to reflect an adaptive response of the CNS to the hypoxic stimulus. The development of structural proteins and of specific enzymatic proteins, such as those associated with neurotransmission, also appear to be impaired in rats developing at high altitude. For example, acetylcholinesterase activity, indicative of the presence of acetylcholine, a putative CNS neurotransmitter, progressively increases with age in sea level rats but is retarded in high-altitude natives (Timiras and Woolley, 1966; Petropoulos, Vernadakis, and Timiras, 1969, 1970). Changes in intracellular and extracellular cell membranes also seem to represent a possible mechanism by which hypoxia may induce alterations in brain maturation, particularly with respect to the formation of myelin, the outer membrane of some nerve fibers. As is well known, myelin makes it possible for the nerve impulse to travel at a faster rate along the nerve fiber; its rate of formation in various CNS structures follows a specific timetable, characteristic for each animal species, and, thus, patterns of myelinogenesis are commonly viewed as useful indices of brain maturation (Petropoulos, Dalal, and Timiras, 1972).

Although alterations in neurochemical development appear to coincide with those in functional maturation, further studies are necessary to better characterize the nature of the CNS retardation occurring in hypoxic animals. Both from an etiopathological and a preventive or curative point of view, it is important to explore further the primary action of hypoxia in terms of the CNS structures principally affected, the type of neural cell (neuron or glial cell) specifically susceptible, and the cellular fraction or organelle most sensitive to the changed environment, so that the defect responsible for altered protein synthesis and retarded functional development of the CNS may be precisely identified at the tissular, cellular, and molecular levels.

Endocrine development

In view of the close relationship between CNS and endocrine development, it is possible that retarded brain maturation in rats born at high altitude may be a cause or a consequence of retarded endocrine development also observed in these animals and discussed elsewhere in this booklet. Delayed maturation of the hypothalamus, for example, may retard the formation and release of hypothalamic releasing factors and, hence, the secretion of pituitary hormones (Timiras and Woolley, 1966; Petropoulos, Garcia, Kragt, and Timiras, 1972; Lau and Timiras, 1972). This explanation would also account for the impairment observed in growth hormone secretion, implicated, in turn, in subnormal body growth of high-altitude rats, as well as the alternations found to occur in gonadotropin secretion and reflected in delayed sexual maturation and abnormal sexual function. On the other hand, the decrease in thyroid function observed in hypoxic animals may also contribute to the delay in brain maturation, for it is well known that thyroid deficiency at a critical period in early brain development induces severe mental retardation (cretinism) in both humans and animals.

The study of CNS/thyroid interactions in animals exposed to high altitude is being actively pursued, not only because of our theoretical interest in elucidating the mechanisms underlying delayed brain maturation in these animals, but also because of the positive clinical significance of such research. In this respect, hormonal treatment represents but one of several interventions possible in dealing practically with the neurological manifestations of hypoxia. Our studies at the White Mountain Research Station have demonstrated that increasing the sensory input of hypoxic animals during early CNS development is capable of restoring to normal or near-normal a number of functional parameters of CNS activity (Petropoulos, Vernadakis, and Timiras, 1970).

Indeed, the hypoxic animal, characteristically retarded in many aspects of its development, serves as a useful model for testing the efficacy of various agents in reversing or preventing such developmental abnormalities. In addition to the therapeutic use of hormonal and sensory stimulation at critical time periods, other approaches may also be profitably investigated, such as those involving pharmacological and nutritional intervention.

METABOLIC STUDIES

F. Duane Blume[1]

The energy required to maintain body processes is derived from a complex series of chemical reactions in which oxygen plays an essential role. Thus, a reduction in the availability of oxygen, such as occurs at altitude, deprives the system of the means of reoxidation of intermediates which is vital in the chemical transformation of energy. For this reason, investigators have undertaken extensive studies of the metabolic changes resulting from both acute and chronic exposure to high altitude.

One might expect the primary effect of exposure to a low-oxygen environment to be a direct alteration of the electron transport system, where oxygen plays its key role. Hencken (1958) examined the level of cytochrome c, a key intermediate in the system and found little or no change in various tissues of rats exposed to 3,800 m at the Barcroft Laboratory. On the other hand, he did observe that while the lactate and pyruvate concentrations in the liver were higher at altitude, the ratio (L/P) of the two intermediates remained unchanged. He suggested that these higher concentrations but normal ratios represent a shift in steady state along with a possible failure of the liver to convert lactate to glycogen.

Glycogen levels

The glycogen content of the liver together with the blood sugar level have frequently been used as indications of the overall state of carbohydrate metabolism in the body. The liver glycogen value is considered to denote the level of the body stores of glucose, while the blood sugar level represents the balance between the rate of tissue glucose utilization and the ability of the liver to maintain blood sugar level within normal limits.

Timiras *et al.*, (1958) undertook an investigation of the glycogen levels and blood sugar values of rats exposed to altitude at the Barcroft Laboratory for varying periods. During short-term exposures, the liver glycogen content of fed rats was observed to vary widely; the initial reduction was followed by a return to normal values after three days. Thereafter, relatively little change was noted in liver glycogen until the length of exposure had exceeded six months, at which time the values were significantly lower. Interestingly, F_2 rats born and raised at altitude had lower liver glycogen values than their sea-level counterparts. Hyperglycemia was noted during the acute period as well, but returned to normal values within a few days. The initial increase was thought to result from either an increased glycogenolysis or a depression of cellular glucose utilization.

The possibility that the lower glycogen values are a result of insufficient food intake was not supported by the studies of Timiras *et al.* (1958), which showed that restrained animals infused with glucose at high altitude demonstrated the same general glycogen changes as were seen in the animals fed *ad libitum*.

Early studies

In a preliminary study to a broader investigation of the changes in carbohydrate metabolism in mice, Blume and Pace (1967) found that the liver glycogen levels were lower during the first few days at altitude, returned to near normal values during the next two weeks, and finally fell to a reduced level thereafter. The conclusion was drawn that the initial loss is a generalized response to an acute stress, and that the chronic reduction resulted from an overall adjustment in steady state induced by the hypoxia. A significant hypoglycemia was also measured after the second week of exposure.

In an attempt to pin point the specific changes occurring in carbohydrate utilization, Blume and Pace (1967) examined the rates of oxidation of several ^{14}C-labeled glycolytic intermediates in the intact animal at altitude. The results indicated that while intermediates of small molecular size—glycerol, pyruvate, acetate, and succinate—were not affected by the 30-day exposure to hypoxia, the oxidation of the hexose compounds—glucose and glucose-l-phosphate—were markedly altered at the end of the experimental period, suggesting that an alteration occurs in the hexose portion of the glycolytic sequence. Other experiments using specific ^{14}C labels in either the one carbon or six carbon positions of glucose indicated a reduction in the pentose pathway activity as well.

Subsequent studies by Blume and Pace (1969) showed that while the oxidation of labeled glucose to $^{14}CO_2$ was reduced, the distribution of the label was increased in liver, muscle and heart tissues. The increase was noted in both the glycogen and nonglycogen fractions of the tissues. It was suggested that the rapid rise in glycogen-labeling combined with a lower total glycogen content could represent an increased turnover of this pool. The specific nature of changes involving the hexose compounds gave some indication that the alteration might involve the phosphorylating steps of that portion of the glycolytic sequence.

ADP/ATP ratio

Cipriano and Pace[2] measured the cellular levels of various glycolytic intermediates in the liver tissue of

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[2] Cipriano, L. F., and N. Pace. Glycolytic intermediates and adenosine phosphates in rat liver at high altitude (3,800 m). Am. Jour. Physiol. 225:393–98, 1973.

rats during the first 60 days of altitude exposure. They found very sharp decreases during the first three hours of exposure in the cellular levels of adenosine triphosphate (ATP), glycogen, uridine diphosphoglucose and 6 phosphogluconate and concomitant increases in the levels of glucose, glucose-6-phosphate, fructose-1,6-diphosphate, pyruvate, lactate and adenosine monophosphate (AMP). This combination of changes indicates that acute hypoxia increases glycogenolysis through the activation of the liver enzyme, phosphorylase, decreases pentose pathway activity, and facilitates the formation of fructose-1,6-diphosphate which is the rate limiting reaction in glycolysis. After six hours of exposure, the levels of all intermediates stabilized at new values and remained relatively constant for the duration of the exposure.

The ratio of adenosine diphosphate (ADP) and ATP has been used as an indication of the cellular level of respiration. Cipriano and Pace found that the ADP/ATP ratio increased during the first three hours, suggesting increased respiration. In view of the findings of Kellogg *et al.* (1956) that oxygen consumption is unchanged at altitude, it was suggested that the ratio change might be due to the establishment of a new steady state resulting from alterations in the reoxidation of the cytochromes in the electron transport system, although no changes have been observed in the enzyme activities of the cytochrome reactions. The adjustments in the levels of the various glycolytic intermediates reflect the overall effects which occur in response to this ratio change. It was concluded that the changes noted in the glycolytic sequence were necessary in the establishment of a new metabolic steady state at altitude.

The fact that carbohydrate metabolism was significantly affected by hypoxia suggests possible alterations in the utilization of protein and fats as well. Blume (1969) and Pace conducted tests using labeled palmitate, alanine and aspartate. Results showed that while the amino acids were metabolized normally, the fatty acid was oxidized to CO_2 at a faster rate and thus contributed to the increased glycogen labelling in liver, muscle, and heart. This evidence supports earlier observations by other investigators that hypoxia induces the mobilization of the body stores of fat; it also indicates an increase in gluconeogenesis as a result of a greater availability of fat metabolites.

In summary, the results of the studies conducted to date have clearly shown that hypoxia induces a shift in the metabolic steady state. The changes begin during the first hour of exposure and stabilize after several weeks at altitude. While the most significant changes have been observed in metabolism of carbohydrates and fats relating to the sources and transformation of utilizable energy, the primary locus which produces these changes is still unknown.

PLANT ECOLOGICAL RESEARCH IN THE WHITE MOUNTAINS

Harold A. Mooney[1]

The White Mountains of California and Nevada offer unparalleled opportunities for plant ecological research. The plant communities that cover the mountain slopes are all comparatively simple because of the severity of the environment and consequently are subject to easy analysis. The plants present in the range represent extremes of adaptive types from those which can tolerate the heat and drought of the low-elevation deserts to those which persist in the alpine, where temperatures are high enough for growth only during a very brief period in the summer.

The area's steepness brings these plant forms close together for easy study, and the good road system along with the helicopter service make them even more accessible. The centrally located, well-equipped mountain laboratories provide convenient bases of operation for studies of all types from descriptive to experimental. The long-term weather records available for these station sites offer a superb context in which to place the results of ecological studies. Finally, the presence of plants which are unique in almost any context, such as the bristlecone pine, and of the vastest expanse of alpine tundra in the far west, make the White Mountain region extremely attractive for plant ecological research investigators.

The flora

The comprehensive flora of the White Mountains listing about 800 plant species by R. M. Lloyd and R. S. Mitchell (1973) will considerably ease the task of plant-oriented research investigators. It contains supplemental sections on the geology of the range by V. C. LaMarche, as well as a general description of the plant communities and vegetation by myself. The flora is predominantly Great Basin in nature, particularly at mid-elevations, although the range lies in close proximity to the Sierra Nevada. The effective rain-shadow caused by the Sierra produces arid climates which support one of the few comprehensive Great Basin biota in California.

An herbarium of the White Mountain flora, located at the Crooked Creek Laboratory, provides a convenient aid for identification of unknown material.

Vegetation patterns

In addition to the generalized descriptions of the White Mountain vegetation found in the Lloyd and Mitchell book, detailed accounts of certain of the vegetation zones have been published. The pinyon woodland, the vegetation which occupies the mountain slopes between the approximate elevations of 6,500 to 9,500 feet, has been studied by St. Andre, Mooney, and Wright (1965). This vegetation type, which characterizes vast areas in the Great Basin, is unique in the high elevations of the White Mountains. The St. Andre study describes the composition of this vegetation type throughout its elevational extent. Although the pinyon forest appears to have recently increased its elevational range, trees of this species (*Pinus monophylla*) are now near their environmental limits, since they form dwarfed trees, or krummholz, at their upper limits. There is an anomalous treeless zone of approximately 1,000 feet between the upper limits of the pinyon forest and the lower limits of the bristlecone pine forest. The zone between these forest types, historically unstable, has provided unique habitats in which unusual assemblages of plants can persist. For example, large hybrid populations of *Cercocarpus* occur in this area (Brayton and Mooney, 1966).

It is, of course, the subalpine bristlecone-limber pine forest which has attracted the greatest attention of botanists. The great age of the bristlecone pine has provided a valuable key to the interpretation of paleoclimates, as will be discussed. The subalpine forest is also of interest because the component species assume a striking pattern, which is related to the geological substrate mosaic in the region. As one example, the bristlecone pine is abundant on dolomitic soils, and is generally poorly represented on quartzitic sandstone and granitic soils. Wright and Mooney (1965) have studied this patterning and concluded that the capacity of bristlecone pine to grow in the low nutrient (yet more mesic) dolomitic soils, where few competitors can persist, is an important component determining this pattern. This study as well as that of Billings and Thompson (1957) give information on the population structure of the bristlecone-limber pine forest which occurs between the elevations of approximately 9,500 and 11,500 feet. These studies, in combination with others (Ferguson, 1968), indicate that bristlecone pine is successfully reproducing itself in these habitats at the present time, as it has been for at least 7,000 years.

The alpine environment and vegetation in the White Mountains extends from approximately 11,000 feet to the summit of White Mountain Peak and has been explored in a number of studies (Mooney, St. Andre, and Wright, 1962; Mooney and Johnson, 1965; Mitchell, La Marche, and Lloyd, 1966; Mooney, 1966; Mooney, Strain, and West, 1968). One interesting feature of this region is the sharp juxtaposition of several

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Left: C. Wesley Ferguson, graduate student, University of Arizona, obtaining a core from a piñon pine tree to determine its age. July, 1955.

geological substrates throughout a wide elevational range—a feature which offers the opportunity of evaluating the interaction of climate and soil type in the determination of plant distribution. One general pattern observed is that alpine plants extend to much lower elevations on the white, cooler dolomitic soils than on the adjacent dark sandstone soils (Mooney, St. Andre, and Wright, 1962). A detailed study of the distribution of two closely related alpine species has shown how complex the environmental controls on plant distribution can be in these environments (Mooney, 1966). Basic differences in soil color cause profound dissimilarities in habitat moisture, temperature, and nutrient availability, which, in turn, control distributions.

Bristlecone pine: a research tool

The exciting discovery in the White Mountains of the oldest known living organism, the bristlecone pine, by Schulman (1956, 1958) has been recently chronicled by Ferguson (1968), and intensive work throughout the years by investigators from the University of Arizona's Tree-Ring Laboratory, starting with Schulman, has been exceptionally productive. Ferguson has been able to extend the bristlecone pine "chronology" back 7,100 years, on the basis of wood remnants. These chronologies are of great importance in a variety of contexts in addition to the primary one of paleoclimatic interpretation. For example, dated wood fragments have been utilized to calibrate the radiocarbon dating technique and will undoubtedly play a large role in resolving the problem of whether ^{14}C production has varied through time.

The studies of Fritts (1966, 1969) have been major contributions to the science of dendrochronology. They have successfully interrelated environmental variation, physiological response, and tree-ring growth. Further, Fritts has developed statistical techniques which have given firm foundation to interrelationships between tree-ring variability and past climatic events.

LaMarche, also of the Tree-Ring Laboratory, in a series of interesting studies utilizing bristlecone pine chronologies, has been able to calculate rates of slope erosion (LaMarche, 1963, 1968), as well as determine how timberline has fluctuated in response to past climatic change (LaMarche, 1967). Further, he has made an ecological analysis of habitats which support the oldest bristlecone pines (LaMarche, 1969). These sites are the driest available within the regions of temperature tolerance of the species.

There have been several studies on the physiology of bristlecone pine, and these have added to our understanding of how this species has successfully survived the severe White Mountain environment (Wright, 1963; Wright and Mooney, 1965; Mooney, West, and Brayton, 1966; Schultze, 1966; Schultze, Mooney, and Dunn, 1967). Probably two of the most important physiological features of this plant related to its survival is the very long time it maintains its needles—often in excess of 20 years—and the reduction in nonphotosynthetic tissue, by bark die-back, with excessive age (Wright and Mooney, 1965). These trees are photosynthetically active only during the brief summer period, and then at a very slow rate. The shorter growing season which persists at somewhat higher elevations than those at which the pine occurs probably would, in itself, limit the distribution of this species, since an insufficient amount of carbon could be gained to maintain growth (Schultze, Mooney, and Dunn, 1967).

No doubt, continued study of the White Mountain bristlecone pines will produce further important scientific results.

Physiological plant ecology

The availability of diverse life forms at White Mountain, all within short distances of each other, has stimulated a number of studies in comparative physiological plant ecology. One of the first field studies of comparative gas exchange of plants under controlled temperature conditions was made in the alpine and desert regions of the White Mountains (Mooney, Wright, and Strain, 1964). This study was followed by an analysis of the influence of environment on carbon dioxide exchange capacity (Mooney and West, 1964). Plants were reciprocally moved between desert and subalpine environments and the effects on photosynthetic capacity monitored. The important findings to emerge from this study were that plants could acclimate within large limits to thermal regimes quite unlike those in which they normally thrive. These results have led to a large number of investigations into the mechanisms and significance of photosynthetic thermal acclimatization in plants. West (1969) has concluded, for example, that the capacity of big sagebrush, *Artemisia tridentata,* to undergo significant photosynthetic acclimatization is a major factor in the widespread distribution of this species.

Using a research design similar to that of the transplant experiments described above, it was found that plants do not acclimate to different environmental CO_2 concentrations (Mooney, Strain, and West, 1968).

An analysis of the *in-situ* water use of plants from different environments showed no relationship between habitat aridity and water conservation by plants (Mooney, Brayton, and West, 1968). Many desert species, for example, have considerably higher water losses than plants from more mesic, higher elevation habitats. These paradoxical results can be explained on the basis of the activity cycles of the plants. Those desert plants with high water consumption are also fixing carbon at a rapid rate during the brief period when water is available. These species become deciduous when the drought ensues. In contrast, evergreen species which tolerate the drought and which have low transpirational losses do so at the expense of a low rate of carbon fixation.

This brief summary of some of the botanical studies which have been carried out during the past twenty years in the White Mountains are illustrative of the kinds of problems that have been pursued so successfully, as a result both of the combination of unique and diverse plant types and communities and the excellent facilities and logistics for research provided by the White Mountain Research Station.

GEOLOGICAL STUDIES

Valmore C. LaMarche, Jr.[1]

To workers in many research fields, the White Mountains are simply a convenient high-altitude platform. To a geologist, the platform itself—including details of geological structure, materials, and surface finish—has long been of great interest. The rocks of this mountain range have been studied for clues to such important geological problems as the nature and location of the boundary between Precambrian and Cambrian times, nearly a half-billion years ago. Strata in the southern White Mountains and nearby Inyo Range form the type section of rocks of Lower Cambrian age, and serve as the reference point for dating rocks of this age throughout the world. The granitic rocks of the northern White Mountains have played a major role in a long-standing geological controversy. Some of these rocks were thought to have originated by a process known as "granitization," whereby sedimentary rocks are transformed to granite deep in the Earth's crust. Although early studies in the White Mountains were widely cited to support this concept, more recent work by Emerson (1959*a,b;* 1960*a,b;* 1966) has cast doubt on its validity. The range also has a great deal to offer to the geologist interested in more recent events and in modern-day geological processes. Certain kinds of rock weathering, soil formation, mass movement, and erosion can be studied to advantage here, where a cold, dry climate has operated for a long time in extensive areas of unglaciated high-altitude terrain. The ancient bristlecone pines, some reaching ages of more than 4,000 years, provide valuable records of geological events and climatological trends.

If the high altitude facilities of the White Mountain Research Station have not been as extensively used by geologists as by other scientists, it is simply because the nature of geological studies usually requires widely scattered temporary base-camps rather than permanent laboratory space. However, many of those doing geologic mapping in the area, such as Emerson (just cited) Krauskopf,[2,3] Nelson,[4,5] Crowder,[6] and Hall (1964), have stayed at, or made occasional visits to the high-altitude laboratories in recent years. Other workers, some with more specialized interests, have relied more heavily on the Station. Beaty (Kesseli and Beaty, 1959; Beaty, 1959, 1960, 1963, 1968) has studied historic flooding, gully development, and other geological processes, and is currently working on high-altitude patterned ground features, using helicopter support. Powell (1963) has worked on the landforms, vegetation and other features of the range. LaMarche (1963, 1965, 1967, 1968, 1969; Mitchell, LaMarche, and Lloyd, 1966; LaMarche and Mooney, 1967; Adam, Ferguson, and LaMarche, 1967) has studied soil erosion, weathering, and glaciation as well as certain aspects of the bristlecone pine. He is now studying evidence for past climatic changes at the upper treeline. Geological-ecological studies carried out by Marchand (1968) included vegetation plots at Crooked Creek Laboratory. Samples of high-altitude soils have been studied by Cameron (Cameron and Conrow, 1969; Cameron, 1969*a,b*) with emphasis on the soil biota.

Despite the long history of geological studies (see "Guide to the Geology" in Lloyd and Mitchell (1973) by V. C. LaMarche), there are many intriguing problems remaining to be investigated in the White Mountains. Some of the topics that could be investigated in more detail include the rates and processes of rock weathering, the mechanisms and rates of downslope movement of rock and soil, and the reasons for the formation of large, Arctic-type frost features at high elevations in contrast to miniature patterned ground formed at lower elevations. The history of sediment deposition and erosion along the major streams draining the White Mountains could be profitably studied using volcanic ash horizons for dating and correlation. Continued attention will probably be given to the timing and mode of emplacement of the granitic rocks, and to the fossils contained in the Lower Cambrian and Precambrian strata.

It is likely that the White Mountain Research Station will play an increasingly important role in future geological and related research in the White Mountains. Some of the research topics mentioned previously will require sophisticated instrumentation, research support personnel, and continuity of effort over long periods. The availability of utilities, space, and logistic support at the high-altitude laboratories will encourage research into some of these problems.

[1] Valmore C. LaMarche, Jr., is Associate Professor of Dendrochronology, University of Arizona, Tucson.

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[5] Nelson, C. A. Geologic map of the Blanco Mountain quadrangle, Inyo County, California. U. S. Geol. Survey Geol. Quad. Map GQ-529, 1966.

[6] Crowder, D. F. and M. F. Sheridan. Geologic map of the White Mountain Peak quadrangle, California. U. S. Geol. Survey Geol. Quad. Map GQ-1012, 1973.

PHYSICAL STUDIES

Ralph A. Nobles[1]

Most of the work in the physical sciences performed at the white Mountain Research Station has been concerned in some manner with cosmic radiation, a phenomenon which in the broadest sense includes all particulate and electromagnetic radiation of extra-terrestrial origin. The atmosphere is quite strongly absorbent to this radiation, except for a few "windows" such as in the optical and radio frequency regions. Hence, the advantage of observing cosmic radiation at high altitude instead of at sea level is that significant increases in intensity can be realized without losing the advantages of ground-based operations.

Cosmic ray research is generally concerned only with the more energetic portion of the cosmic radiation—that above several million electron volts energy. Such research can be divided into two main categories. First are studies of the nature of the radiation itself and its interactions with local matter and fields; this, in essence, is nuclear physics. Second are studies of cosmic radiation for the information it can impart about its origin and the medium through which it has traveled, that is, geophysics and astrophysics. Cosmic ray research is often motivated by interest in both categories, but usually one dominates.

Nuclear physics

In the early years of the discipline, interest was centered mainly on nuclear physics; as a matter of fact, most of the fundamental particles known today were first observed in the cosmic radiation. Indeed, the rapid advancement in high-energy nuclear physics beginning in the early 1950's was due not only to the advent of the high energy accelerator, but also to the ground work already laid by previous cosmic ray research. However, it turned out that the convenience, controllability and greater intensity of the new machine-produced radiation was so attractive to the high-energy nuclear physicist as to temporarily cause a virtual abandonment of the cosmic ray field. Evidence of this situation is demonstrated by the fact that 1950 and 1952 saw the publication of the only three White Mountain cosmic ray papers of the decade. The first, by Seriff *et al.* (1950), was on cloud-chamber observations of new unstable cosmic ray particles, and the second, also in 1950, by J. R. Green (1950*a*, *b*) was on penetrating showers in carbon. The third, in 1952, by H. K. Ticho (1952), discussed the absorption mean-free-path of large hard showers in air. Other than reports concerning the research station and its environment, this group of papers comprise the earliest White Mountain research publications.

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It was not until 1963, however, that the next physics paper appeared, a paper by Palsedge and Baum (1963), on the altitude dependence of the longitudinal distribution of atmospheric Cerenkov radiation. This paper, principally geophysical in nature, exemplifies the changed emphasis in cosmic ray research.

Cosmic ray research

In August of 1965, Lockheed Palo Alto Research Laboratory's newly developed cosmic ray neutron multiplicity monitor (Nobles, Newkirk and Walt, 1964) arrived at Barcroft for an anticipated two-month period of operation. This monitor is a geophysical research instrument which observes the intensity and energy spectrum of the incident nucleonic cosmic radiation. After an initial period of operation, it became apparent that the Lockheed monitor operating at Barcroft constituted an exceptionally powerful research tool, so much so that the monitor is now permanently located at Barcroft and is known to the cosmic ray world as the "White Mountain multiplicity monitor." In the beginning, the operation of the monitor was supported jointly by Lockheed and the National Aeronautics and Space Administration; however, present support is solely by Lockheed as part of the company's basic research program. There are no proprietary or classified aspects of the work, and all results are published in the open literature. Significant contributions resulting from the monitor's operation at Barcroft concern the shape of the cosmic ray energy spectrum, the spectrum variations during cosmic ray disturbances, the nature of the modification of the primary spectrum by the atmosphere, and definitive information on the relationship of certain cosmic ray intensity increases and the earth's magnetic field ring currents. Results were published by Nobles, Newkirk, and Reynolds (1965), Nobles *et al.* (1966*a,b;* 1967*a,b*), Noblés and Wolfson (1968), Wolfson and Newkirk (1968), Wolfson *et al.* (1968, 1969).

Astrophysical studies

A different aspect of the production of neutrons by cosmic rays was reported in a paper by Yamashite, Stephens, and Patterson (1966). These experimenters studied the ambient production of neutrons in the environment at Barcroft, rather than production in a target inside a monitor, as in the Lockheed work. Their results are of interest with respect to neutron backgrounds in nature, naturally induced radioactivities, and the neutron albedo of the atmosphere.

In 1967, a series of four papers appeared in Physical Review Letters reporting work done at Barcroft on the cosmic microwave radiation background. The first was by W. J. Welch *et al.* (1967), on measurements of the cosmic microwave background temperature at 1.5 cm wavelength. Next were two papers by Princeton physicists, D. T. Wilkinson (1967) on measurements at 8.56 mm wavelength, and Stokes, Partridge, and Wilkinson (1967) on similar measurements at 3.2 cm and 1.58 cm wavelengths. The last paper was by Ewing, Burke, and Staelin (1967), of M.I.T., on measurements at 9.24 mm wavelength. These experiments were motivated by the search for observational evidence concerning the "Big Bang," or what amounts to the same thing, the "Primeval Fire Ball" hypothesis of the beginning of the universe as described by G. Gamow[2] and R. H. Dicke *et al.*[3], respectively. If this hypothesis is valid, an isotropic background of cosmic microwave radiation with the spectrum of a 3 °K blackbody would be expected throughout the universe. The White Mountain measurements, as well as those of others, tend to support the hypothesis; however, the evidence cannot be considered conclusive. An excellent review article by R. B. Partridge (1969) describes the current status of this interesting subject.

The cataloging of twenty years of physical sciences research cannot be concluded without mentioning the work of Terjung *et al.* (1969), who made radiation balance measurements on White Mountain peak on a typical mid-July day and reported daily amounts of solar heat radiation and net radiation values exceeding any previously reported in the literature.

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[3] Dicke, R. H., P. J. E. Peebles, D. G. Roll, D. T. Wilkinson. Cosmic blackbody radiation. Astrophys. Jour., 142: 414–19, 1965.

In summary, research at White Mountain in the physical sciences, i.e., physics, geophysics, astrophysics, and the like, had a strong beginning followed by an almost complete cessation for nearly a decade. The renewal of physics research starting in 1964 was occasioned by the growth of interest in astrophysical studies.

Moderate-cost research potential

From a physicist's point of view, the past two decades of physics research at White Mountain seems rather meager, especially considering the great potential of such a high-altitude laboratory site. However, this will probably change in the future, as the completion of the projected underground power line with the resulting increased dependability of electrical power will greatly enhance the utility of the Barcroft Laboratory to all users, particularly the physicist. Also, with the cutback in "big science" and general diminishing of research support, greater use will probably be made of the opportunities for moderate cost research possible at a mountain altitude station.

* * * * *

One of the most pleasant aspects of the White Mountain Research Station is the opportunity it affords for contact between scientists from diverse disciplines. Such opportunities are unfortunately rare in these days of increasing specialization in science.

Left: Wade Patterson, Lawrence Laboratory, Berkeley, and his brother, removing sheets of gold foil from between layers of cadmium and paraffin to examine them for cosmic ray tracks. Summit Laboratory. August, 1958.

ASTRONOMY AND METEOROLOGY

David D. Cudaback[1]

Astronomical observations from the earth's surface are, of course, deeply influenced by weather and climate. This has become even more important as observations are made into the region between optical and radio wavelengths, where absorption by atmospheric water vapor is all-important. Weather also affects the "life" of large astronomical instruments and the transportation of personnel required for their operation.

Inspection of the Climatic Atlas of the United States[2] shows a maximum of clear sky, total hours of sunshine, and maximum temperature, along with a minimum of precipitation, at Yuma, Arizona. These conditions prevail in diminishing quality over roughly a triangle with one point at Yuma and the other points approximately at Bishop, California, and El Paso, Texas. The line between Bishop and El Paso goes near Las Vegas, Nevada and Prescott, Arizona. I call this region the dry triangle.

However, the solar radiation at ground level is a maximum of 819 cal cm^{-2} day^{-1} at Inyokern, California, in June and the relative humidity is a minimum of 20 per cent there and at Death Valley, instead of at Yuma. Therefore, on this broadest view of climate we could expect White Mountain to be a good place for astronomical observation, being near to the driest part of the dry triangle.

The above atmospheric parameters are measured usually at valley level, but astronomical observations must be made from stations higher in the atmosphere. The astronomical needs are at least for minimum water vapor overhead, minimum scattering of visible light, and minimum random refraction of light by small temperature fluctuations in the air close to the ground. These conditions would be best met by an isolated mountain (wishfully a slender probe) located in the dry triangle, preferably in the Inyokern-DeathValley-Las Vegas region. The first two of the above conditions definitely improve with altitude (and the random refraction may improve), and White Mountain at 14,246 feet is the highest peak in the dry triangle. The Sierra Nevada are not included since they form the wall which helps to keep the triangle dry.

Weather

Weather measurements have been made continuously since 1949 at the Crooked Creek Laboratory, and since 1953 they have been made at the Barcroft Laboratory. These are summarized in a highly useful report which is the foundation for planning almost any experiment at White Mountain (Pace, Kiepert, and Nissen, 1971). These weather reports have been used specifically for some interpretations of relationship between temperatures and snowfall by D'Ooge (1955*a*, *b*). These are major peaks in the snowfall at mean daily temperatures of −11 and −4°C. The first peak is expected from laboratory measurements of nucleation, and the second peak is clearly attributable to silver iodide cloud seeding experiments upwind in the Sierra Nevada.

Unfortunately, the price to be paid for the good conditions on a mountain during fair weather includes the severe conditions during bad weather. As long as there is sufficient time to do significant work under good conditions, it is worth the effort of coping with the bad.

Water vapor

Oxygen and nitrogen are uniformly mixed in the earth's atmosphere, so they are exponentially distributed with altitude at a scale height of ~ 8000 meters (the scale height is the altitude difference over which the density changes by a factor of *e*). Therefore, at the summit of White Mountain, their pressure is 58 per cent of that at sea level. This reduction is helpful to most astronomical observations, but is not as spectacular as the reduction of water vapor. Not uniformly mixed, this vapor varies with latitude, continental features, and local topography, and it has a much smaller scale height than does the atmosphere as a whole. Various determinations of the scale height of water in the free atmosphere range from 1,600 to 2,600 meters. However, on White Mountain several techniques give scale heights between 500 and 1300 meters. In other words, a small change of altitude makes a big change in water vapor compared to the change in atmospheric pressure, and the local orographic phenomena at White Mountain make this change bigger than in the free atmosphere.

At the time of this writing, a major survey is being made of many atmospheric conditions affecting astronomical observations. This has frequently shown less than 0.5 mm of precipitable water vapor above the summit of the mountain. In addition to this extremely low quantity of water vapor, the low atmospheric pressure reduces the pressure broadening of the water spectral lines. This gives the effect of sea-level absorption by about one half the actual amount of precipitable water vapor.

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[2] Environmental Data Service, Environmental Science Services Administration, U. S. Department of Commerce, June 1968.

A very preliminary analysis of the statistics of the quantity of water vapor shows that out of all the clear nights of the year, there is less than 1 mm for 50 per cent of the time, and less than 0.5 mm for 10 per cent of the time.

Cosmic fireball observations

Although these measurements of water vapor are just now under way, the expectations of small amounts of water has caused a highly important series of astronomical measurements to be made in the past. These measurements have contributed extensively to understanding of the cosmic fireball, otherwise known as the three-degree background radiation. This radiation is interpreted to be left over from the original, explosive expansion of the Universe about 10 billion years ago. Because the radiation falls upon us from all directions, it is not necessary to isolate a small range of direction with a telescope. The measurement is made simply by pointing upward the flared end of a rectangular metal pipe, called a wave guide. Radio waves from the incredibly distant origin of the Universe flow into this wave guide and are detected at its lower end.

In 1967, four papers were published which jointly very well defined the spectrum of the fireball from 8.56 mm to 3.2 cm, as measured from the Barcroft Laboratory (Welch *et al.*, 1967; Wilkinson, 1967; Stokes, Partridge and Wilkinson, 1967; Ewing, Burke, and Staelin, 1967). This spectrum fits that of a blackbody with a temperature of 2.7 ± 0.2 °K. A delightful review article summarizes all the fireball work from various stations up to 1969 (Partridge, 1969).

After this basic specification of the fireball radiation was made, questions arose about its uniformity over a range of angle and wavelength. The distribution in angle, measured at the Barcroft Laboratory with a wavelength of 3.75 cm and a resolution of 12° of arc, was found to be uniform to the level of about 0.1 per cent of the 2.7 °K temperatures, but there was a residual anisotropy below that level (Conklin, 1969). This anisotropy can be interpreted as due to Doppler shift caused by the motion of the sun with respect to the local supercluster of galaxies. Furthermore, this indicates that this local supercluster does not have a large velocity with respect to the Universe as a whole. This is a pretty impressive conclusion to achieve from pointing a wave guide at the sky from the top of a mountain.

More recently there have been a series of measurements made of the cosmic fireball during brief times when sounding rockets are above the atmosphere. These have suggested major spectral features, which are sharply varying with wavelengths in the region shortward of one millimeter. However, recent more careful measurements made at the Barcroft Laboratory have shown no evidence for these features (Mather, Werner, and Richards, 1971). This shows the occasional advantage of observations made from a mountain instead of from space. Although the remaining atmosphere above the mountain is a great hindrance, the ability to make careful, repeated, well-controlled measurements can sometimes overturn the apparent disadvantages.

The above sub-millimeter spectral measurements have also established that the 730 micron transmission at Barcroft is about 65 per cent, 850 micron about 75 per cent, and 1,000 micron about 85 per cent, because of the low amount of water vapor there.

Stellar and planetary observations

Another class of astronomical observations based on low water vapor was started in 1962 at the Barcroft and Crooked Creek laboratories. This program made the first exploration of the flux of stars and planets at 10 microns wavelength using a small, conventional telescope. The first measurements at this wavelength outside of the solar system where astronomical objects are fainter than those inside, was a major achievement (Westphal, Murray, and Martz, 1963; Murray and Wildey, 1963).

Among the measurements made inside the solar system, there was a very important determination of lunar nighttime temperatures (Murray and Wildey, 1964). The combination of new techniques and dry atmosphere enabled them to be followed down to 105 °K, which is appreciably colder than was earlier possible. No overall difference in thermal properties could be found between maria and highlands, but local regions showed the higher temperatures associated with more compacted material than the average.

Light scattering in clear sky

The scattering of light caused by small particles and liquid droplets in the atmosphere affects astronomical observations in two ways. For ordinary stellar measurements the scattering simply reduces the amount of light reaching the telescope. For measurements involving intense gradients of brightness, however, the scattering transfers light from bright regions to faint ones. The extreme case of this is in measurements of the sun's corona. When the direct light from the sun is eclipsed by the moon, the brightness of the sky within one tenth of a degree from the sun is about 10^{-9} of the normal brightness of the sun's photosphere, while the brightness of the corona is about 10^{-6} of the photosphere. At ordinary astronomical observatories, and no eclipse, the sky in the same region is commonly around 10^{-3} the sun's brightness.

A survey of sky brightness was made in 1949 at the Crooked Creek Laboratory at White Mountain, at Sacramento Peak, New Mexico, and at Climax, Colorado (Roberts and Trotter, 1950). This survey clearly showed that White Mountain was the superior site, having a sky brightness less than 3×10^{-4} of the sun an average of 5.3 hours per day over a year. The next best site had 3.8 hours per day in this category. Since the sky must be totally free of even thin cirrus clouds to give low scattering, this number is much more conservative than the average number of "clear" hours per day.

The outstanding result from that survey was that during October of 1949 at Crooked Creek there was an average of six hours per day with sky brightness less than 3×10^{-5} of the sun, while the best at other sites was less than four hours per day in that category.

During the current survey of atmospheric properties, the sky brightness seen from the summit of White Mountain appears to be the same as that measured at Crooked Creek 22 years ago. However, there is clearly visible air pollution in the Owens Valley now, and that may well increase the scattered light above the mountain in the future.

This low scattering of sunlight, of course, enables more of it to reach the surface of the earth. The low amount of water vapor enables good re-radiation of solar energy after it heats the earth and is re-emitted in the infrared. The amount of solar radiation falling on the surface (Terjung *et al.*, 1964) at the summit of White Mountain is as great as, if not greater than, any other amounts recorded in the world. On a day in mid-July, a total of about 940 calories/cm^2 falls on a horizontal surface at the summit, while about 800 calories/cm^2 falls at nearby Inyokern which is 12,000 feet lower. The radiant sky temperature or brightness temperature of the sky has a minimum in different directions according to the position of the sun. During the above measurements in July, the highest value of this minimum was 260 °K and at sunrise it was 245 °K. It presumably is much lower at night.

During the same week that the above measurements were made at the summit, a more detailed study of energy and moisture balances was made at a lower site located between the Barcroft and Crooked Creek laboratories (Terjung *et al.*, 1969). This revealed somewhat higher radiant sky temperatures at the lower site, as would be expected from the greater amount of water vapor there. These studies of energy flow point out the extreme variations in radiation climate felt by living organisms at high altitude due to the high incident radiation and cold sky. Indeed, the alpine tundra undergoes one of the greatest energy fluctuations observed on this planet.

"The quiet gathering phenomena . . ."

The suitability of White Mountain for an astronomical observatory site has already been described by Dr. Pace in the first article herein and by Zwickey (1950).

The earlier described report on sky brightness near the sun (Roberts and Trotter, 1950) further recommended use of White Mountain; this was not followed up because of logistic problems—nor were the 10-micron measurements (Murray and Wildey, 1963; 1964) followed up after their initial success. At that time, the observational requirements of infrared astronomy did not need the exceptionally low water vapor at the summit, so further measurements were moved to other mountains with paved roads.

In the late 1960's, a survey was started to study the atmospheric properties of a 13,400-foot plateau between the Barcroft Laboratory and the summit. It was hoped to place there an infrared telescope for studies of planets. This study was shut down prematurely for lack of funds, but a photographic survey of cloud cover was carried to a very useful result (O'Connor, Welch, and Tayeb, 1968). Some measurements were made of water vapor, both from the ground and from radiosonde balloons. During the period July, 1967, to March, 1968, there was less than 25 per cent cloud cover for 35 per cent of the entire period. During night and morning hours this occurs 50 per cent of the time. There are months when 80 per cent or more of the nighttime hours are totally clear. The water vapor measurements were scattered, but they indicated the same conditions as the current measurements. This includes scale heights as low as 800 meters.

An excellent, forward-looking paper was presented by Kuiper (1970*a*) on the needs for a high site for infrared and millimeter astronomy. This paper described many mountain sites, including White Mountain. Further study of White Mountain produced a companion paper (Kuiper, 1970*b*) which discussed the outstanding advantages of this mountain. These papers have stimulated and encouraged the more extensive survey now under way.

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Fans of White Mountain, such as this author, see it as a profoundly important locale for the future of several frontier fields of astronomy. This includes the explosive, relativistically energetic phenomena of quasars and expanding galaxies and the quiet, gathering phenomena of origins of molecules and maybe even of life.

A RECORD OF PUBLICATIONS (ALSO LITERATURE CITED HEREIN) CONCERNING WORK AT WHITE MOUNTAIN RESEARCH STATION 1950 TO JANUARY 1, 1973

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Copies of this publication may be obtained from Director, White Mountain Research Station, Building T-2251, University of California, Berkeley 94720, California.

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