INVITED PERSPECTIVES IN PHYSIOLOGICAL AND BIOCHEMICAL ZOOLOGY

Laurence Irving: An Appreciation

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ABSTRACT

Laurence Irving (1895–1979) contributed significantly over five decades to the development of environmentally oriented physiological studies. He is best known for his investigations of the physiology of diving mammals, the respiratory properties of fish blood, and cold adaptation and acclimatization in poikilotherms and homeotherms, including man. Beyond his own research contributions, Irving benefited American comparative physiology through his key roles in the immigration of Per F. Scholander and Knut and Bodil Schmidt-Nielsen to the United States. The Irving-Scholander research collaboration provides a substantial legacy for comparative physiology. Laurence Irving's administrative contributions include service as the first scientific director of the Arctic Research Laboratory at Barrow, Alaska, and as the founding director of the Institute of Arctic Biology at the University of Alaska, Fairbanks. These units have assured the implementation of his philosophy of combining laboratory and field studies in the investigation of environmentally oriented physiological problems. Laurence Irving was an ardent advocate for Alaskan research, and his efforts were an important help in the advancement of science in the state.

Introduction

In 2005, I spoke before the physiological ecology group that meets annually at the White Mountains Research Station of the University of California. My talk traced events that led to the remarkable post–World War II expansion of ecologically oriented physiological studies at United States institutions such as my alma mater, the University of California, Los Angeles. In preparing this presentation, I was impressed by the importance of the contributions of Laurence (Larry) Irving (Fig. 1).

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Most members of my audience were generally familiar with the Irving–Per F. Scholander legacy in polar biology (Elsner 2000), but few knew of the total scope of Larry's professional accomplishments, which have played a key role in shaping physiological ecology as we know it today. Thus, I concluded that an article focusing on the total span of his contributions would be useful in fostering a renewed appreciation of Larry's importance both to environmentally oriented physiology and to comparative physiology generally. I was further motivated to write about him because of a friendship dating from his sending me an encouraging note in 1955 about my first research proposal to the National Science Foundation, which he had reviewed.

Professional Career

Laurence Irving was born in Boston on May 3, 1895.[1] He received his AB from Bowdoin College in 1916 and his AM from Harvard the next year. His further studies were interrupted by military service as an infantry lieutenant in the American Expeditionary Force and Army of Occupation during and shortly after World War I (Irving 1945). Following his return to civilian life, he enrolled at Stanford and completed a PhD in physiology in 1924. After a further year there as an instructor, he spent 1925–1926 in Frankfurt, Germany, working with the physiological chemist Professor Gustav Embden on a National Research Fellowship. Embden was well known, of course, for his studies of carbohydrate metabolism and the chemistry of muscle contraction and was the first to discover and link all of the steps in the conversion of glycogen to lactic acid. Two immediate dividends from Irving's fellowship were short reports on muscle chemistry (Irving and Deuticke 1927; Irving and Fischer 1927), and he was involved with this topic for several years after that (e.g., Bastedo and Irving 1928; Manery et al. 1935). He returned to Stanford as an assistant professor in 1926 and moved the next year to the University of Toronto as an associate professor, reaching full professor in 1934. (In 1934–1936, after Gustav Embden's death, Irving reciprocated for his year in Germany by securing the immigration of the professor's daughter Maja to Canada, allowing her to escape the virulently anti-Semitic policies of the Nazis. He appears in this period to have helped other German Jewish scientists as well [T. D. Simpson, undated term paper, "Dr. Laurence Irving: Alaskan pioneer

Figure 1. Laurence Irving (1895–1979). Photo courtesy of the Institute of Arctic Biology, University of Alaska, Fairbanks.

scientist in comparative physiology and arctic biology," University of Alaska, Fairbanks].)

In 1937, Larry became professor and chair of the Department of Zoology and director of the newly established Edward Martin Biological Laboratory at Swarthmore College. He soon hosted August Krogh (1920 Nobel Prize in Physiology or Medicine) for lectures on comparative respiratory physiology, which led to a classic book on this topic (Krogh 1941). Larry's association with this distinguished Danish scientist had other consequences. The first of these, in 1939, involved procurement of a Rockefeller Fellowship for Scholander that allowed him to leave Europe at the beginning of World War II and join Irving to pursue their mutual interest in the physiology of diving mammals (Scholander 1990). One of the storied collaborations in comparative physiology resulted.

Larry Irving served physiology, and especially comparative physiology, in a variety of ways beyond his research. While at Toronto and Swarthmore, he taught in the Marine Biological Laboratory physiology summer course from 1931 to 1940, serv-

ing as course director over most of that period. Larry also was a member of the editorial boards of the *Journal of Cellular and Comparative Physiology* (1932–1955), *Biological Bulletin* (1939–1950), and *Physiological Reviews* (1940–1947). He was a trustee of the Marine Biology Laboratory at Woods Hole, Massachusetts (1935–1947), and of Biological Abstracts (1941–1944). Additionally, he participated in three divisions of the National Research Council in the years just before the United States' entry into World War II.

Even before that entry, Irving undertook projects evaluating cold protection provided by military clothing, aerobic support for high-altitude flight, and carbon monoxide hazards in aircraft and winter shelters (Irving 1945). One result was development and production of several devices for gas analysis by the group he established at Swarthmore. Also in 1942, Detlev Bronk, coordinator of research in the Office of the Air Surgeon, U.S. Army Air Force, proposed to Irving that he form a physiological section in that branch of service to test equipment for increasing the effectiveness of flight personnel (Irving 1945). In 1943, Larry reported to the Air Force Proving Ground at Eglin Field, Florida, as a major and chief of the Physiological Test Section. Scholander, a captain, and two others from Swarthmore joined him there. Subsequently, he served as chief physiologist, Aeromedical Laboratory, at Wright Field, Ohio, leaving the service as a lieutenant colonel in 1946.

After their return to Swarthmore, Irving and Scholander went to Scandinavia during the summer of 1946. They visited August Krogh and participated in discussions of a proposed institute at the University of Oslo for research on nutrition, biochemistry, and animal physiology. They met Knut and Bodil (Krogh's daughter) Schmidt-Nielsen in Norway and invited the couple to Swarthmore as research associates (Schmidt-Nielsen 1998). The Schmidt-Nielsens arrived in the United States in late 1946. Their introduction to the Sonoran Desert in the spring of 1947 involved field testing certain analytical methods (Schmidt-Nielsen 1998). This was followed over the next two summers by the classic work of the Schmidt-Nielsens and collaborators on the water metabolism of desert rodents (Schmidt-Nielsen and Schmidt-Nielsen 1952), a problem that Larry Irving is credited with suggesting (Schmidt-Nielsen et al. 1948).

Some of Larry's greatest contributions took place in Alaska. He had become interested in arctic research while in the Air Force, probably due in part to Scholander (Scholander 1978). Serendipitously, he was planning an arctic research project at a time when the Office of Naval Research (ONR) was exploring the possibility of establishing a research facility at Barrow, Alaska. In 1947, Larry began a two-year term as the first scientific director of the Arctic Research Laboratory (ARL; later the Naval Arctic Research Laboratory) at Barrow under a contract he helped develop between Swarthmore and the ONR (Reed 1969; Norton and Weller 2001; Schindler 2001). He and his six-person research team arrived at Barrow on August 6, 1947 (Schindler 2001). Beyond involvement in the work of this

team, Irving was responsible for implementing the first contractual relationship between ONR and the sponsoring educational institution, which in this initial case was Swarthmore College, and for developing governance procedures for ARL and effective working relations with naval and contractor personnel involved in the U.S. Navy's oil exploration operation based in Barrow (Reed 1969). Irving made other fundamental contributions to scientific operations at ARL. Scholander and he initiated a pattern of research involving teams of several individuals, which became a hallmark of investigations at this facility (Norton and Weller 2001). Moreover, Larry soon recognized the research potential of members of the local Inuit community, with their keen observational powers and accurate recollection of events of natural historical significance (Brewster 1997).

In 1949, Irving became chief of the Physiology Section, Arctic Health Research Center (U.S. Public Health Service) in Anchorage, Alaska. This allowed him to continue his work with arctic animals. In 1962, he joined the University of Alaska, Fairbanks, as founding director of the Institute of Arctic Biology (IAB), serving in this capacity until 1966. The University's interest in establishing such an institute had coincided with Larry's procurement of external funding for a Laboratory of Zoophysiology on campus. This laboratory, based on the concept underlying Krogh's Laboratory of Zoophysiology in Copenhagen (P. R. Morrison, personal communication) and established with the collaboration of Peter R. Morrison of the University of Wisconsin, Madison, became the initial component of IAB, which formally opened in October 1962.[2] After 1966, Irving served as IAB's advisory scientific director until his retirement in 1974. The Institute continues today, and it is fitting that it is housed in the Irving Complex (Irving I and associated buildings) on the Fairbanks campus of the University of Alaska. Throughout his years in Alaska, Larry was an ardent advocate for Alaskan and other high-latitude research and was instrumental in the establishment of the Alaska Division (after 1982, the Arctic Division) of the American Association for the Advancement of Science. He became the division's first president in 1951–1952 and served a second term in 1971. As part of his efforts, he played an important role in the development of the Alaskan (later, Arctic) Science Conference, serving as an alternate on the steering committee for the initial conference

held in Washington, DC, in 1950 (Angel 1951) and as a leading participant in the second (Irving 1951*b*) and third (Irving 1954) conferences, which were held in Alaska. He continued to participate in many of the subsequent conferences in this series.

Larry Irving's scientific and administrative contributions were recognized in several ways beyond his being appointed to various leadership roles and the naming of the Irving Complex in his honor. He received a distinguished service award from the U.S. Public Health Service (1956), an honorary MD from the University of Oslo (1956), and honorary DSc's from Bowdoin College (1959) and the University of Alaska (1968). His memory and that of his close collaborator, friend, and son-in-law Scholander are sustained by IAB's annual Laurence Irving–Per F. Scholander Memorial Lecture. Laurence Irving died at the age of 84 on November 20, 1979 (*Fairbanks (AK) Daily News-Miner*, November 24, 1979).

Research

Introduction

Laurence Irving began publishing in 1924 (Irving 1924; Irving and Becking 1924), and his bibliography includes approximately 270 titles. These deal principally with physiology, natural history, and anthropology, though some examine the chemistry of seawater and the influence of biological processes upon it (Irving 1925, 1926, 1936). Some of Irving's titles represent abstracts of research presented at scientific meetings, but most involve substantial reports of original research and contributions to symposia and monographs. I examine here the publications summarizing Irving's applied research and those for which he is best known in comparative physiology. I also describe his forays into natural history and anthropology, to illustrate the full breadth of his interests. His principal contributions comprise several segments, some of which overlap chronologically.

First Segment: Studies of Diving Physiology and Respiratory Transport

Irving's interest in respiratory physiology is evident in the first major segment of his research, covering approximately 1933–1943. An important portion of this segment was studies of the physiology of diving, principally in mammals. He presented a lecture at the Marine Biological Laboratory in 1933 that reviewed the ability of mammals to survive without breathing (Irving 1933). He then published an expanded version of this that covered both diving birds and mammals (Irving 1934). This work summarized information on submergence periods by these animals and suggested a prominent role for the nervous system in integrating the organic responses permitting diving mammals, in particular, to tolerate extended periods of apnea. Larry also speculated that the limited amount of nitrogen carried in the lungs of diving whales would not create a risk for

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[2]The 1962 report by a committee (D. S. Farner [chair], A. D. Hasler, R. H. McBee, F. A. Pitelka, C. L. Prosser, D. L. Ray, P. F. Scholander, W. C. Steere, and F. W. Went; "Report to the President of the University of Alaska by the Committee for the Study of the Feasibility of the Establishment of an Institute of Arctic Biology at the University of Alaska") recommending the establishment of an institute of arctic biology on the Fairbanks campus of the University of Alaska was generously given to me by Dr. Brian M. Barnes, the IAB's current director. My abbreviated account of the establishment of this unit is based primarily on conversations with Dr. Peter R. Morrison and on an unpublished 1989 manuscript by Dr. George C. West, "Institute of Arctic Biology: the first twenty-five years," which was also provided to me by Dr. Barnes.

caisson disease upon resurfacing (Irving 1935). Subsequently, while still at the University of Toronto, he launched a study of the physiology of the harbor seal (*Phoca vitulina*).[3] The first part, conducted at the Atlantic Biological Station, St. Andrews, New Brunswick, analyzed the water balance of this animal, concluding that the preformed water in its fish diet and metabolic water sufficed to offset losses in the marine environment (Irving et al. 1935*a*). The metabolism of harbor seals and their adjustment to enforced dives also were studied (Irving et al. 1935*c*). Respiration by these animals was typically periodic in character and relatively unaffected by breathing 5% CO_2. However, it was accelerated by 10% CO_2. Generally, no special physiological mechanisms relevant to diving were evident, and responses of the seals in this activity appeared only quantitatively different from those of mammals generally. Nonetheless, the high sensitivity of their vasomotor control would provide a basis for redistribution of blood flow favoring the brain and heart during submergence. Another report (Irving et al. 1935*b*) concerned the respiratory properties of the blood of the harbor seal, which, aside from a somewhat higher oxygen capacity, resembled those of other mammals, a conclusion reinforced by subsequent determination of oxygen equilibrium curves for the blood of the American mink *Mustela vison*, American marten *Martes americana* (Scott et al. 1939), and red fox *Vulpes vulpes* (Irving et al. 1939*b*).

In pursuit of comparative information on diving, Irving (1937) studied the American beaver (*Castor canadensis*). He found that lung inflation rapidly decreased the perfusion of the muscles but increased perfusion of the brain, circulatory changes that apparently prepare the animal for endurance of asphyxia by conserving oxygen for that organ. A study of muskrats (*Ondatra zibethicus*), cats, dogs, rabbits, and beavers documented similar circulatory redistribution, with lung inflation and arrest of breathing (Irving 1938*a*). The principal efferent pathway for the muscular response involved the sympathetic nervous system. Neither the carotid sinus nor the vagus depressor system was an essential afferent. The basis of the cerebral vascular response was more obscure, but the cervical sympathetics, carotid sinus regions, and vagus depressor nerves were unnecessary for its occurrence. Irving (1938*b*) also found relative insensitivity to inhalation of CO_2 in muskrats and beavers; fractions up to 10% affected neither breathing, cardiac action, nor blood pressure.

After his 1937 move to Swarthmore College, Irving reviewed the respiration of diving mammals (Irving 1939). Unusual for its time, the review had some phylogenetic concerns. Storage of oxygen by diving mammals appeared inadequate for its indiscriminate use by all tissues, and no shift of metabolism could compensate for oxygen lack. Irving proposed that differential

control of distribution of this gas might serve to maintain the brain, with less sensitive tissues or those with a strong capacity for anaerobic metabolism surviving without oxygen. He also noted that effective control of the circulation reduces muscular perfusion as it increases perfusion through the brain. Incidental control of the heart and reduction of muscular activity would enhance the effectiveness of the adjustments. However, Irving reemphasized that the main adjustments of divers differ only quantitatively from those of land mammals.

The arrival of Scholander at Swarthmore College in 1939 produced a substantial expansion of research on diving physiology. This led to several publications by him, S. W. Grinnell, and Irving, an effort Irving referred to as "a very pleasant collaboration" (Irving 1942, p. 12). Again, the harbor seal was the principal subject (Irving et al. 1941*c*, 1942*c*; Grinnell et al. 1942; Scholander et al. 1942*a*, 1942*b*), but studies were also conducted on the bottle-nosed dolphin *Tursiops truncatus* (Irving et al. 1941*b*) and the West Indian manatee *Trichechus manatus* (Scholander and Irving 1941). The research required substantial logistics. The seal work was done at the Bureau of Commercial Fisheries Biological Laboratory (U.S. Fish and Wildlife Service) at Woods Hole, Massachusetts. A pilot study of two porpoises obtained with professional help off Hatteras, North Carolina, allowed design of equipment and procedures on the Swarthmore campus. The main part of the study took place at the Marine Studios Biological Station, Marineland, Florida, where the work on the manatees was also done.

Irving et al. (1940) provided a useful synopsis of the results for the harbor seal, bottle-nosed porpoise, and West Indian manatee from enforced dives under restraint. Ventilation, O_2 consumption, differences between O_2 and CO_2 exchange, certain circulatory variables, and lactate concentrations were examined. The animals all showed circulatory changes, primarily bradycardia (greatest in seals) and changes in muscular perfusion. Irving (1963*a*) later recalled incidental observations made by his group in 1940 demonstrating bradycardia in humans during apnea in air and in diving. The results on the seal and manatee, especially, indicated an adjustment to diving in which blood flow decreased through the muscles, which remained aerobic at first, using intrinsic oxygen reserves. Reliance on anaerobic formation of lactate followed. In seals, a steady decline in body temperature and an estimated halving of metabolic rate (Scholander et al. 1942*b*) would extend the aerobic period. The small part of the circulation maintained during a dive would sustain aerobic metabolism for key tissues such as the brain. Oxygen in arterial blood was depleted during a dive, and the end of this process marked the termination of submersion. Lactate did not appear in the blood to any extent until the recovery period following an animal's resurfacing. It then flooded the blood of seals and manatees, with a concurrent reduction in CO_2 concentration. Periodic sampling indicated that the predive O_2 content of about 5 vol% in the muscles was nearly all consumed within 5 min but was restored quickly

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[3] In this article, I use currently accepted common and scientific names of the species discussed. These occasionally differ from those used by Irving and his colleagues.

in recovery. Lactate appeared to rise only after the myoglobin was reduced. Thereafter it increased rapidly. Surprisingly little lactate was formed by porpoises during dives.

Shortly before the United States' entry into World War II, the Swarthmore group did additional work on responses of mammals to suspension of breathing. Irving, Scholander, and Grinnell traveled to the Barro Colorado Biological Area in the Panama Canal Zone to investigate respiration of two- and three-toed sloths *Choloepus hoffmanni* and *Bradypus variegatus* (Irving et al. 1942*b*) and nine-banded armadillos *Dasypus novemcinctus* (Scholander et al. 1943*d*). Interest in the sloths was prompted by their low body temperature, slow movements, and a reported ability to recover after breathing had been arrested for 20 min, a performance matching that of some diving mammals. Sloths showed a poor utilization of ventilatory O_2 and low alveolar Pco_2. Unlike diving homeotherms, they displayed neither a reflex apnea in the course of immersion in water nor any proclivity for diving. However, they did resemble these other animals during suspension of breathing in showing some circulatory restriction involving bradycardia as well as a reduction of metabolic rate from the resting level.

The nine-banded armadillo was of interest due to its habit of vigorously burrowing when threatened. Oxygen equilibrium curves and chemical analyses of blood showed it capable of contracting a substantial O_2 debt over 3–4 min of violent struggle during suspended breathing. Bradycardia (to one-third to one-half of resting rates) occurred despite the struggle, though heart rate tended to rise after 5 min of asphyxia. Struggles with the suspension of breathing under such stress produced metabolic rates equivalent to 10–15 × resting values. Understandably, recovery from bouts of asphyxia by armadillos involved increased heart rate (200–300 beats/min vs. 70–100 beats/min during rest). Scholander et al. (1943*d*) felt these observations were relevant to natural situations, for breathing could be hampered by sand and dust during emergency digging. The observations on both this armadillo and the sloths assisted in distinguishing between special capacities and widely shared mammalian attributes in analysis of the physiology of diving.

The studies by Irving and his associates using restrained seals and other mammals in enforced dives proved useful in characterizing the so-called dive reflex and the maximal capacities for diving possessed by these species. Only later did work with unrestrained homeotherms, often using more powerful instrumentation (see Kooyman 2004), document how these capacities are actually employed in voluntary dives (reviewed by Costa and Sinervo [2004]). Bradycardia, restriction of the circulation, and lowered metabolism still occur in freely diving individuals but generally at more modest levels than those seen in animals during longer, enforced dives. Most dives by unrestrained animals such as the Weddell seal *Leptonychotes weddelli* (Kooyman et al. 1980) are brief enough to be accomplished aerobically, and the prevalent view is that this pattern of not exceeding the

aerobic dive limit is typical of diving birds and mammals generally (Ponganis and Kooyman 2000).

In this segment of his research, Larry Irving also participated in studies of respiratory transport in fishes. E. C. Black and he (Black and Irving 1938) analyzed the effects of CO_2 on the transport properties of the blood of three freshwater species from Ontario lakes (carp *Cyprinus carpio*, common [white] sucker *Catostomus commersonii*, and bowfin *Amia calva*). They found that this gas reduced the O_2 combining power of the blood of these fishes even at Po_2 as high as 150 mmHg. However, hemolysis virtually eliminated this effect, even at Pco_2 approaching 100 mmHg. In a study at the U.S. Fisheries Laboratory at Woods Hole, Massachusetts, R. W. Root, Black, and Irving found (Root et al. 1939) that hemolysis largely eliminated the powerful action of CO_2 on the oxygen affinity and capacity of the whole bloods of the three marine fishes (toadfish *Opsanus tau*, tautog *Tautoga onitis*, and northern sea robin *Prionotus carolinus*) used in Root's classic study (1931). The action of hemolysis was especially strong in the first two species. In all three, the results indicated an important role for the erythrocytes themselves in the transport of respiratory gases (Root et al. 1939). The effects of CO_2 and hemolysis were explored further in the tautog by Root and Irving (1941), who found that CO_2 and lactic acid had similar actions on O_2 affinity and capacity of its blood. This led them to suggest that this resulted from the effect of these compounds on pH (Root and Irving 1943). Hemolysis rendered the tautog's blood insensitive to CO_2 at tensions approaching 100 mmHg. However, at higher tensions, hemolyzed blood showed the same responses regarding O_2 affinity and capacity as whole blood, leading to the postulate that pH is lower within erythrocytes than in the plasma of intact blood (Root and Irving 1943).

Irving et al. (1941*a*) also measured the oxygen capacity and analyzed the inverse relation between oxygen affinity and temperature in the bloods of three salmonid fish. Oxygen affinity at 15°C in the absence of CO_2 was nearly uniform among the brook trout (*Salvelinus fontinalis*), brown trout (*Trutta trutta*), and rainbow trout (*Salmo gairdneri*). However, at 5°C and a normal venous Pco_2 of ca. 10 mmHg, mean P_{50}, in this case describing unloading O_2 tension, respectively averaged 29, 32, and 39 mmHg in these fish. The order at this Pco_2 and 25°C differed, with P_{50}'s of 39, 41, and 54 mmHg in the rainbow trout, brown trout, and brook trout, respectively. Unlike the results of Black and Irving (1938) on other freshwater fish, hemolysis in trout blood only slightly diminished the CO_2 effect (Irving et al. 1941*a*).

Even with all his other activities in the late 1930s, Larry Irving found time in 1939 to organize a project to track changes in the oxygen transport characteristics of the blood of Atlantic salmon (*Salmo salar*) as they moved from brackish to fresh water during spawning runs on the Gaspé Peninsula of Canada. He enlisted E. Benditt, a medical student at the University of Pennsylvania, and P. R. Morrison, who had just completed his

junior year at Swarthmore (P. R. Morrison, personal communication), for the actual field work. They found reduced O_2 capacity, cell volume, P_{50}, and osmotic pressure in the blood as the fish moved from brackish to fresh water. A large reduction in oxygen capacity, that is, a Root effect, was noted in the presence of CO_2 and a Po_2 of 150 mmHg. In this case, hemolysis did not reduce this effect substantially (Benditt et al. 1941).

In the studies of fishes, interspecific differences were noted in the blood regarding oxygen affinity, oxygen capacity, and response of these variables to CO_2 and temperature. In several species, these differences revealed much about respiratory tolerances, capacity for activity, and/or distribution (Black et al. 1939; Irving et al. 1939a, 1941a). The potency of the CO_2 effect documented for whole-fish blood also prompted an experiment relevant to buoyancy control in fish having swim bladders. With fully oxygenated blood of brook trout under approximately 2 atm pressure, Irving and Grinnell (1939) demonstrated the release of O_2 in the presence of CO_2. They concluded that exposure of a continuing supply of oxygenated blood to CO_2 could provide a secretory action contributing to regulation of swim bladder volume.

Second Segment: Applied Research

Laurence Irving participated in the development of a method for determining CO_2 content of muscle (Ferguson and Irving 1929) and of several devices for measurement of the respiratory properties of blood and metabolic rate (Irving and Black 1937; Scholander et al. 1943a, 1943b; Irving et al. 1947). He also collaborated with Scholander in developing a procedure for gas analysis using very small blood samples (Scholander and Irving 1947; Scholander et al. 1947).

Some of the research Larry did for the United States armed forces was published in the open literature. Two studies (Irving et al. 1942a; Scholander et al. 1943c) analyzed how CO is formed when small stoves are used in tents or snow houses. Another (Nickerson et al. 1945) described the benefits of sandal use by soldiers in reducing foot infections in warm humid environments. Other work dealing with the properties of insulating materials was summarized in reports to the Committee on Aviation Medicine of the U.S. Air Force and did not reach external circulation. However, it evidently did serve to instill in Irving a recognition of the need for a cold weather research laboratory, which would lead him to the Arctic after the war.

Third Segment: Thermal Acclimatization and Responses of High Latitude Organisms to Cold

Before military service in World War II, Larry Irving participated in studies of the effects of temperature and season on the metabolism of some poikilotherms living in the vicinity of Woods Hole, Massachusetts. The cunner (*Tautogolabrus adspersus*), a fish, had slightly higher rates of oxygen consumption

at temperatures from 0° to 30°C in winter than in summer (Haugaard and Irving 1943). However, the compensation was incomplete, for cunner in winter still showed markedly depressed metabolic rates and activity at low temperatures. The extent of seasonal acclimatization was also examined in two crustaceans near Woods Hole. The upper thermal limit for sand (mole) crabs (*Emerita talpoida*) was approximately 10°C higher in summer than in winter. Metabolic comparisons were complicated by the larger size of individuals obtained in summer. When this difference was taken into account, the metabolic rates of winter sand crabs at 3°C in winter were approximately four times the summer values at this temperature. The thermal compensation associated with this seasonal metabolic adjustment was sufficient to allow sand crabs to continue growth and activity throughout the colder months of the year (Edwards and Irving 1943b). On the other hand, no such seasonal adjustment to temperature was evident in the beach flea *Talorchestia megalophtalma* (Edwards and Irving 1943a).

Larry Irving and colleagues' work in Alaska is the body of research for which my cohort of graduate students knew him best. Scholander was the primary scientist in the studies at ARL in the late 1940s, but it is important to note that these studies depended on Larry's procurement of funding and the development of appropriate organizational and administrative structures and that they benefited from his wise participation. Elsner (2000) reviews the accomplishments of the group Irving led in ARL. Its major effort in physiology dealt with the thermal responses of arctic and tropical homeotherms and poikilotherms as well as lichens. Within the various taxonomic groups involved, the species selected for comparison often were not closely related, which hindered detailed analyses in the absence of modern phylogenetic perspectives. Nevertheless, considerable insight was gained about the capacities of organisms for operating at warm or very cold temperatures.

Perhaps the best known of the publications by Scholander, Irving, and others from ARL are those dealing with homeotherms, principally larger mammals (Scholander et al. 1950a, 1950b, 1950c). The original research and a broad review of the pertinent literature reported in these articles produced the conclusion that the superior cold resistance of arctic forms evolved only through factors regulating heat loss, notably fur and tissue insulation. Neither body temperature nor basal metabolic rate (BMR) were regarded as adaptive to climate (Scholander et al. 1950a). The insulation of arctic foxes and Eskimo dog pups was so effective that the minimum temperatures that could be imposed at Barrow (ca. −30°C) still appeared to be within the animals' respective thermal neutrality zones, (TNZ; Scholander et al. 1950b).[4] They were taken to the Naval Research Labo-

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[4] However, it should be noted that Fuglesteg et al. (2006) report the lower boundary of the arctic fox's zone of thermal neutrality to be −7° and 5°C during winter and summer, respectively. They suggest that the discrepancy between their and Scholander et al.'s (1950b) results is due to elevated metabolic rates during measurements of the latter group's animals.

ratory in Washington, D.C., for more severe cold exposure, and temperatures of $-70°$ to $-80°C$ did induce shivering. Development of a model that was described as based on Newton's law of cooling allowed prediction of critical thermal gradients (the difference between body temperature and the lower boundary of the TNZ, the latter being the lower critical temperature, T_{lc}) that approximated empirical values in several species (Scholander et al. 1950a). This model figured in thermoregulatory studies of homeotherms for the next several decades.

Scholander, Irving, and their collaborators at ARL also measured the resting oxygen consumption of a heterogeneous assemblage of arctic and tropical poikilotherms from Alaska and from Cuba and Panama, respectively (four fishes, eight crustaceans, two mollusks, and a spider in the arctic group; seven fishes, seven crustaceans, four insects, and a spider in the tropical one). As noted above, the absence of close evolutionary relationships between most members of the arctic group and their respective tropical counterparts restricted detailed comparisons. Nevertheless, major differences suggesting climatic adaptation were evident. The temperature range tolerated by the aquatic arctic forms extended from approximately $-2°$ or $0°C$ to no more than $15°$ or $20°C$, whereas that of their tropical counterparts was $15°–35°C$. Thus, metabolism-temperature curves were conspicuously displaced toward colder temperatures in members of the former group. However, the thermal compensation indicated by this would be incomplete, for, after differences in body mass were taken into account, the rates of oxygen consumption by the arctic species at their habitat temperature ($0°C$) were only one-third to one-tenth those of the tropical forms at theirs ($30°C$). Despite this, Scholander et al. (1953b) noted that activity levels of the high-latitude forms near freezing approximated those of the animals from the warmer water. To account for this, the authors raised the possibility of an enhanced capacity for activity metabolism in the arctic forms. Unlike the aquatic situation, metabolic responses of terrestrial insects differed little geographically when corrected for differences in body mass.

The Irving-Scholander group at ARL also determined the relation of oxygen consumption to temperature in 19 species of arctic and 10 of tropical lichens. Generally, the data for representatives of the two sets of species overlapped at all temperatures, providing no indication of climatic adaptation (Scholander et al. 1952). However, within the families Stictaceae and Peltigeraceae, the arctic forms respired at higher rates than members of the same taxon from the tropics, suggesting some thermal compensation for cold.

At ARL, the Irving-Scholander group also undertook a major excursion into the area of cryobiology by investigating physiological processes in frozen arctic plants and animals (Scholander et al. 1953a). Seven of the eight species of vascular plants studied became dehydrated in winter. Chironomid larvae frozen into the ice also were found to be somewhat dehydrated. They

could be thawed and refrozen experimentally without apparent injury. The body fluids of these larvae froze sufficiently that reduction in the amount of unfrozen water remaining produced concentrations of solids that varied approximately in proportion to the decrement in temperature below $0°C$. This fluid water was not in a supercooled state. Respiratory gas exchange at temperatures down to $-26°C$ occurred in five species of vascular plants, four species of lichens, and the chironomid larvae. The Q_{10} for oxygen consumption rose abruptly as temperatures cooled to $+2°$ to $+5°C$, reaching a relatively high value that persisted to $-26°C$. Scholander et al. (1953a) believed this would contribute to extended survival, even at relatively high but persistent subfreezing temperatures. They noted that many animals and plants spend winter frozen into ice, where they would normally respire at a measurable rate. This prompted a study of properties of ice that would affect gas exchange. The solubility of air in ice was found to be less than 10^{-3} times that in water. The diffusion of CO_2 through ice was only $1.43 × 10^{-5}$ to $2.50 × 10^{-5}$ times that through water, and O_2 was even slower. The Irving-Scholander group concluded that adequate gas exchange for an animal like a chironomid larva can occur at low temperature and shallow depth, but in thicker ice, at temperatures approaching $0°C$, the situation would become essentially anaerobic.

Further questions about adjustments to cold by mammals and birds occupied Larry Irving after he joined the Arctic Health Research Center in 1949. One project (Irving and Krog 1954) involved determination of body temperatures in a sample of arctic and subarctic homeotherms (22 species of mammals and 30 of birds). Temperatures under a variety of environmental conditions were similar to those of birds and mammals from milder climates. Further observations on birds established that the extent of the nocturnal decline in body temperatures in representatives of seven species from four avian orders that were exposed to temperatures of $-9°$ to $-26°C$ also resembled that reported for temperate birds under milder conditions (Irving 1955). Irving and Krog (1956) also found that incubation temperatures maintained under cool conditions by seven species of arctic birds from three orders matched those of their temperate counterparts. These observations provided further support for Scholander et al.'s (1950a) view that modification of core body temperature is not an important component of adaptation of persistent homeotherms to arctic cold.

While at ARL, the Irving-Scholander group had considered how birds with unfeathered legs avoid the freezing of these appendages in winter (Scholander et al. 1950c). They had determined that heat loss from the webbed feet of glaucous gulls (*Larus hyperboreus*) was low, and they surmised that the blood flow through them was just sufficient to maintain temperatures slightly above freezing. Irving (1951a) also commented on the ability of gulls, ducks, and various mammals to maintain low peripheral temperatures in the cold. He and J. Krog (Irving and Krog 1955) subsequently reported on surface temperatures

of exposed tissue in the extremities of eight mammals (including caribou and reindeer *Rangifer tarandus*) and nine species of birds. Temperatures of less than 10°C at these sites occurred in the majority of these animals in the cold, and cooling to 0°C was observed in three species. For example, the naked metatarsi of the legs in two glaucous-winged gulls (*Larus glaucescens*) were near 0°C in ambient temperatures of −15° to −20°C. Cold extremities would certainly curtail heat loss, particularly if coupled with the vascular heat exchangers postulated by Irving and Krog (1955).

The peripheral heterothermy observed in the legs of arctic and subarctic gulls in winter led Chatfield, Lyman, and Irving (1953) to examine whether the distal portion of nerves in these appendages showed any special capacities for conduction at low temperatures absent in more proximal segments normally maintained at temperatures near that of the body core. Peroneal nerves excised from herring gulls (*Larus argentatus*) that had been wintering on the Maine coast showed a gradient in resistance to cold, with the distal segments conducting impulses at substantially lower temperatures than the proximal ones. Moreover, the compound action potential reached a maximum at a lower temperature in the former segment than in the latter. Interestingly, no such gradient in temperature response was found in the homologous nerve from the feathered leg of the domestic fowl, in which the distal portion remains warm even at low ambient temperatures (Chatfield et al. 1953). Miller and Irving (1963) also examined the effects of temperature on peripheral nerve function, using ventral caudal nerves from the naked tails of Sprague-Dawley albino rats that had been maintained for a long period at 23°C or outdoors in the cold. The conditions produced tail temperatures of ca. 27°C and near 0°C, respectively. These investigators additionally studied caudal nerves from the naked tails of muskrats obtained in Alaska and Louisiana (Miller and Irving 1967). Only minor differences of doubtful adaptive significance were detected in the in vitro thermal responses of the nerves between the two groups of rats or the two populations of muskrats, despite the differences in thermal history. Thus compensation for cold of the type noted in the peroneal nerves of herring gulls is not universal in peripheral nerves of homeotherms having naked or poorly insulated appendages.

Appendages are not the only site where peripheral heterothermy could be important. Irving studied the thermal topography of swine, which, despite lacking an insulating pelage, can live outside during winter in subarctic Alaska. He reported (Irving 1956) that skin temperature over their shoulders and back varied directly with ambient temperature, reaching stable values as low as 9°C in air at −12°C. Subcutaneous temperatures in the shoulder rose with increasing depth, becoming asymptotic at 38.4° ± 0.5°C 40–70 mm beneath the surface. Activity promptly elevated surface temperature, indicating (*a*) the competence of vasomotor arrangements even at low tissue temperatures and (*b*) the capacity of the superficial tissues for either conserving heat in the cold or facilitating its dissipation during activity. Irving et al. (1956) supplemented the preceding observations with measurements of the metabolism and temperature of two 50-kg boars. The T_{lc}'s of these swine, where insulation should be near maximal, were near 0°C. Below this temperature, the animals appeared to reduce their insulation through phasic relaxation of vasoconstriction in the peripheral tissues. Apparently need of these tissues for perfusion could locally dominate requirements for insulation. However, peripheral heterothermy seemed to give swine an overall insulation similar to that of fur-bearing mammals (Irving et al. 1956).

Larry Irving (1959, 1962) recognized that peripheral heterothermy raised questions about the impact of cooling on the functional capacities and integration of affected tissues. Cooling reduced the conduction velocity and excitability of peroneal nerves in herring gulls (Chatfield et al. 1953). The operation in vivo of the distal and proximal segments of these nerves at very different temperatures and conduction velocities in many situations would seem to present challenges for these birds' information processing and motor functions (Irving 1959). Cooling also reduced the sensitivity of fingers to tactile stimulation in human subjects (Irving 1963*b*). Despite such problems, the tissues involved in peripheral heterothermy do function at lower temperatures, for as Irving (1956) noted, they are visibly sensitive and actively perfused. Moreover, despite their frequent operation at low temperatures, they must grow as well as maintain and repair themselves (Irving 1959). Their successful function depends in some instances on a broad thermal tolerance. For example, caudal nerves of muskrats from both Louisiana and Alaska continued to conduct well-formed action potentials in vitro even when supercooled (Miller and Irving 1967). Local compensatory adjustments seem involved in other cases. Thus, fat from the distal portion of the limbs of several species of arctic mammals as well as the red brocket (*Mazama americana*) remained soft at near-freezing temperatures that solidified fat from the proximal portion of the femur and central body (Irving et al. 1957). Although apparently not a special adjustment for cold due to their presence in the tropical red brocket, the distribution of such low melting point fats in the limbs and feet of the northern mammals would appear advantageous in arctic cold. Furthermore, as noted previously, the metatarsal segment of the peroneal nerve in herring gulls that had been exposed to cold could conduct at lower temperatures than the tibial segment. In this case, exposure of gulls to warmer conditions eliminated the difference (Chatfield et al. 1953), indicating a plasticity of peripheral nerve function in this species.

A study of thermoregulation by some Alaskan mammals and birds at different seasons allowed Irving to return to his interest in acclimatization (Irving et al. 1955). A red fox and porcupines (*Erethizon dorsatum*) showed substantially reduced T_{lc}'s in winter, a change attributed to the animals' thicker winter pelage.

On the other hand, T_{lc}'s were similar between summer and winter in red squirrels (*Tamiasciurus hudsonicus*), a black brant (*Branta bernicla*), and a northwestern crow (*Corvus caurinus*), species in which insulation remained seasonally stable. Basal metabolic rate did not change between summer and winter in any of the species studied. Irving also participated in one of the early studies comparing the characteristics of cold acclimation of albino rats in the laboratory with the winter acclimatization occurring in wild Norway rats exposed to the bitterly cold temperatures of refuse dumps in Fairbanks, Alaska (Krog et al. 1955). The BMR of albino rats exposed to 5°C for 6 wk was 45% higher than that of counterparts living at 30°C and 60% above the value predicted for animals of their body mass. Lower critical temperatures were similar in the 5° and 30°C groups. However, differences in peak (i.e., summit) metabolic rate (PMR) were apparent. Rats that had been living at 5°C reached PMR at −10° versus +10°C for those conditioned to 30°C. Peak metabolic rate was about triple the BMR in both groups but absolutely higher in the cold-acclimated individuals with their greater basal rates. This allowed these latter rats to avoid hypothermia for 2.5 h at −30°C, whereas −10°C was the coldest at which 30°C controls could remain euthermic that long. In contrast, the BMR of winter acclimatized wild Norway rats matched predicted levels and their PMRs were 4.5–6 × BMR, enabling them to withstand lower ambient temperatures than albino rats acclimated to either 5° or 30°C (Krog et al. 1955).

Larry returned to pinnipeds to assess further the role of peripheral heterothermy in heat conservation. Even small harbor seals acclimatized to December conditions at St. Andrews, New Brunswick, increased their metabolic rate by only 20% in ice water (Irving and Hart 1957). Their T_{lc}'s in water and air were 10° and below −10°C, respectively, a difference reflecting the 20-fold greater cooling power of the former medium. Even more impressive, young harp seals (*Phoca groenlandica*) of similar size did not increase heat production in ice water. Neither of these seals is well clad with fur, and their performance in cold water was attributed to the cooling of their superficial tissues, which involved body surface temperatures near 1°C (Irving and Hart 1957). The flexible vasomotor arrangements involved in such cooling also produced rapid warming of these tissues during activity or a change in external temperature. Hart and Irving (1959) supplemented information on thermoregulation of harbor seals in air and water using animals acclimatized to summer conditions near Woods Hole. The T_{lc}'s of the animals in the two media were 2° and 20°C, respectively. Skin temperature at these critical temperatures was near 21°C in each case. Below thermal neutrality, similar metabolic rates were evident at equivalent skin temperatures whether the seals were tested in air or water. This suggested the importance of peripheral inputs in their thermoregulatory control. Comparison of the results obtained for these harbor seals with those from St. Andrews in December (Irving and Hart 1957) revealed

that the summer animals had lower body insulation, higher T_{lc}'s, and warmer skin temperatures for the same metabolic rates below thermal neutrality. This raised the possibility of a seasonal difference in the sensitivity of thermogenesis to peripheral stimuli. Thermoneutral metabolic rate did not differ between summer and winter in these harbor seals.

Peripheral heterothermy also proved important in very young harbor seal pups (<5 wk old) captured at the tip of the Alaska Peninsula, near the northern limit of the range of the subspecies *Phoca vitulina richardi* (Miller and Irving 1975). These individuals had relatively limited fat but short, coarse, wettable hair like that of adults. Nevertheless, they could swim in water at 5°C for several hours without becoming hypothermic and, while wet, tolerate an air temperature of 5°C in a 35-kt wind. These performances were ascribed to a high rate of resting metabolism and to the tissue insulation arising from low peripheral temperatures, particularly in the appendages.

Irving et al. (1962) documented a more localized version of peripheral heterothermy in adult northern fur seals (*Callorhinus ursinus*) from the Pribilof Islands, whose dense waterproof fur provides effective insulation for the main part of the body. Surface temperatures under this fur were no lower than 32°C and exceeded 35°C in six experimental immersions over 2 h. The large flippers of these seals, nearly one-third of their total body surface, served as variable insulators. Surface temperature of these appendages, ranging from 34.0° to 9.5°C, varied directly with ambient temperature, thereby either facilitating the loss of heat at higher temperatures or promoting its conservation in cooler air. Cooling of the flippers in dives was attributed to diminished peripheral circulation associated with bradycardia. The subsequent rewarming during recovery was linked to the restoration of this circulation. Fur seal pups differ from adults, for their natal coat is wettable and affords poor insulation in the water. This and the relatively large surface area of their flippers led to the pups' cooling during occasional immersions. Tolerance of hypothermia allowed them to survive such events. The shift of these pups to aquatic life at 3–4 mo after birth depended on their growth of an adult-style waterproof fur coat and development of effective regulation of their peripheral circulation (Irving et al. 1962).

Two male student members of a religious community who, in the interests of simplicity, went only lightly clothed and shod outdoors in the Alaskan winter gave Irving an opportunity to study facets of acclimatization of Caucasians to cold (Irving 1960c). Exposure of these individuals to temperatures near 0°C when clad only in shorts and a short-sleeved robe evoked mild shivering only after many minutes. Similar treatment of a male unacclimatized to cold soon produced vigorous shivering. Cold exposure of the students led to cooling of both fingers and toes, which then showed slow cycles of warming and cooling. The cooling exceeded that noted in the unacclimatized individual. However, even temperatures below 5°C did not cause the students the pain in digits that were this cold that was

commonly reported by unacclimatized Caucasians. Larry also found that the freedom of the students from such discomfort was accompanied by an ability to detect and locate accurately thermal and other dermal stimuli at skin temperatures as low as 6°C, potentially a valuable defense against frostbite.

Larry Irving participated in several physiological studies of indigenous peoples in the Alaskan and Canadian Arctic (Andersen et al. 1960; Elsner et al. 1960; Irving et al. 1960; Hildes et al. 1961; Hart et al. 1962). Some indications were obtained that Inuits and Indians differed from Caucasian controls in maintaining warmer hands in cold tests. Immersion of the hands of Indians in ice water was accompanied by less pain. Moreover, rewarming after tests was more rapid than in the control individuals (Elsner et al. 1960). Similarly, pain during cooling of the exposed hands of Inuits was absent or minor, though it was marked in most Caucasian controls (Miller and Irving 1962). Representatives of both groups of indigenous people also were less wakeful than the controls while shivering with inadequate bedding during overnight exposures to moderate cold (Elsner et al. 1960; Irving et al. 1960). Inuit hunters were also shown to maintain somewhat higher peripheral temperatures than the controls in overnight tests (Hart et al. 1962). The basis of the various differences in thermal responses of Inuits and Indians relative to controls was not determined. The performance of the two indigenous groups was viewed as less important for dealing with severe cold than their ancestral technology involving shelter, clothing, and wisdom concerning the Arctic (Hart et al. 1962; Miller and Irving 1962).

Fourth Segment: Indigenous People and Natural History

Laurence Irving had a high regard for the indigenous people he met in the Arctic and great respect for their knowledge of the natural world (see "Professional Career"). He discovered that a number of Nunamiut (inland Inuit) in the Anaktuvuk Pass area (Alaska) could not only identify and apply consistent names to various species of birds but also supply details about their habits and migratory patterns (Irving 1953, 1960a). The names bore a close resemblance to those used by Inuits on Baffin Island and Greenland, indicating stability of nomenclature among people who historically had no written language (Irving 1960e). Certain older Indian residents of Old Crow, Yukon Territory, Canada, likewise had an extensive knowledge of their local avifauna (Irving 1958b). Irving recognized the value of the information obtained from native sources, which could provide the biologist with observations "made during a lifetime and in seasons and weather when most scientists remain indoors" (Irving 1958b, p. 118). The Nunamiat played a major role in the research for his monograph on the birds of Anaktuvuk Pass, Kobuk, and Old Crow. Irving (1960a, p. VII) emphasized, "Without their help, existence for us would have been too difficult to permit methodical scientific investigation; thanks to their careful observations, accurate knowledge of country, and ability to travel, our studies proceeded rapidly." Simon Paneak, whom he first met during an ornithological field trip in the Brooks Range of northern Alaska in 1947, was his closest associate among these people (Brewster 1997). The initial employer-employee relationship of these two soon blossomed into a partnership that extended over 25 years and came to involve a fast friendship. Paneak, who was a keen observer, kept a daily field notebook for Irving of bird sightings, weather conditions, and local events, and he also collected eggs and bird specimens.[5] Periodically, Irving lived and traveled with the Paneak family to study birds. Simon Paneak's importance in their partnership is indicated by his being mentioned more than anyone else in Irving's (1960a) monograph. Their bond is further illustrated by Irving's bringing him to various Alaska Science Conferences and by their unprecedented coauthorship of several papers (e.g., Irving et al. 1967b).

Irving's (1960a) monograph is his principal contribution to the natural history of Alaska. It represents more than 12 years of work involving many field trips and, as noted above, extensive interactions with local Nunamiut. Its emphasis on Anaktuvuk Pass reflected the importance of this landscape feature as a major pathway for avian migrants onto the north slope of Alaska. The monograph manifests Irving's approach to arctic biology. He wanted to know about all facets of life in the region, not just the details of individual physiological processes. Accordingly, the work includes not only information on the physiography and climatic history of northern interior Alaska and species accounts for Anaktuvuk Pass, Kobuk, and Old Crow but also analysis and historical consideration of the movement patterns of the migrants considered. The monograph differs from many other regional avifaunas in Irving's inclusion of the physiological data he had such a key hand in gathering into an account of features that contribute to the ability of various birds to meet challenging climatic conditions.

The field work of Irving and his colleagues (Irving 1960d, 1961, 1965; Irving et al. 1970; West et al. 1968a) led to several original contributions to the knowledge of natural history of arctic Alaska. The willow ptarmigan (*Lagopus lagopus*) especially received considerable attention, allowing publication of analyses of migration (Irving et al. 1967b), winter feeding habits (Irving et al. 1967a), morphometrics of birds in the Anaktuvuk Pass area (West et al. 1968b), and geographical variation in body size and mass (West et al. 1970). The various populations sampled differed in body size and mass, but each showed great homogeneity in these features. The birds migrating south through Anaktuvuk Pass tended to segregate by age and sex, with adult males and juvenile and adult females being preponderant in the northern and southern parts of the winter range, respectively, and juvenile males being so at Anaktuvuk.

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[5]Paneak's field journals and the Irving-Paneak correspondence are housed with Larry's personal and professional papers in the archives and manuscript collections of the Elmer E. Rasmuson Library, University of Alaska, Fairbanks.

The Final Segment: The Summation

Larry Irving's publications span more than five decades. He was still producing original work through 1975, but after 1958 many of his publications consisted of reviews and symposia contributions based on his published work. He returned to his roots with a chapter in the respiration section of the *Handbook of Physiology* (Irving 1964*a*). This surveyed respiratory structures in the principal animal phyla and the ventilatory arrangements serving many of them. Detailed treatment of respiration in chordates was included. Irving made a point of documenting the differences in metabolic levels that separate ectothermic and endothermic animals. Approximately one-third of the chapter was devoted to diving birds and mammals, and a number of familiar themes developed by Scholander and him were reprised—relative insensitivity of divers to CO_2, relaxation and reduced metabolism, bradycardia, differential circulation among the various tissues, and sequestration of lactic acid during submergence. This contribution appeared before studies indicating that most birds and mammals that dive typically do so within their aerobic limits (e.g., Kooyman et al. 1980). It retains importance in providing examples of the impressive capacities of many mammals for tolerating submerged periods exceeding their aerobic dive limit.

In the last segment of his career, most of Laurence Irving's chapters in monographs and contributions to conferences and symposia dealt in some manner with temperature regulation and adaptation to cold (Irving 1958*a*, 1960*b*, 1962, 1964*b*, 1964*c*, 1964*d*, 1964*e*). These emphasized the primacy of insulation in the adjustments of larger arctic and subarctic homeotherms to cold and the role of peripheral heterothermy in the thermoregulation of various species. Additionally, his introduction to the chapters on animals in the cold (Irving 1964*e*) in the *Handbook of Physiology* section on adaptation to the environment is noteworthy for its consideration of the evolution of adjustments of homeotherms to cold, which he believed preceded Pleistocene glaciation. His chapter on birds and mammals in the cold in this book (Irving 1964*d*) effectively updated and summarized the work by the Irving-Scholander group at ARL, incorporating additional information on acclimation and acclimatization to cold. Here and in two conferences Irving (1962, 1964*b*) again considered integration in tissues with peripheral heterothermy, as influenced by the effects of variable temperatures on catalytic rates and nerve function. He supplemented these contributions with a semipopular account (Irving 1966*a*) of cold adaptation in homeotherms, whose thermal responses were compared with those of poikilotherms.

Late in his publishing career, Irving returned to aquatic mammals. One contribution (Irving 1966*b*) dealt with the circulatory responses involved in diving reflexes and relied a great deal on the original work by his colleagues and him, which involved measurements made during forced dives. He docu-mented the broad distribution of bradycardia and isolation of the skeletal muscles by vasoconstriction in homeotherms and reptiles during dives. He also described the role of these responses in protecting animals from asphyxia under special circumstances: human infants during birth and certain fish during temporary emergence into air. The review reminds us of the seminal role of Irving and Scholander in defining the full capacities of diving animals for dealing with the challenges of asphyxia.

Larry also authored two chapters on the thermoregulation of aquatic mammals covering marine (Irving 1969) and then freshwater and marine species (Irving 1973). The first chapter treated the thermal characteristics of aquatic environments and reviewed information on conditions within them during the Pleistocene. Irving reiterated his inference (Irving 1964*e*) that mechanisms for cold defense by mammals (and birds) developed before this glacial geological epoch. In both chapters on aquatic mammals, he summarized the distribution of the principal taxa, noting that only present-day dugongs and manatees are confined to warmer regions, whereas pinnipeds and cetaceans have much broader distributions ranging from the tropics to polar regions. Deep-body temperatures of these divers are similar to those of their terrestrial counterparts (Irving 1969), but resting metabolic rates of a limited sample of seals and porpoises appeared high for mammals of their size. The T_{lc}'s of the seals, not surprisingly, were lower in air than water and seasonally appeared to approximate temperatures of the respective media. Larry (Irving 1969) compared the insulation of fur and hair seals, again emphasizing the importance of peripheral heterothermy and vascular heat exchangers in maintaining thermal balance. He discussed the different paths followed by pups of the two types of seal in developing competence for functioning in cold water.

Larry's later chapter (Irving 1973) repeated the various themes explored in 1969 (Irving 1969) and added some new information. It also contains a discussion of the serious heat challenges than can affect certain very well-insulated aquatic mammals (e.g., the California sea lion *Zalophus californianus* and the northern fur seal) when they are active on land. Larry also considered effects of immersion and diving on humans, reviewing information on swimmers of the English Channel, Indians from Tierra del Fuego, Australian aborigine pearl divers, and Korean ama. Training or seasonal exposure appeared to enhance capacities of swimmers or divers for dealing with cold water through mechanisms similar to those in other species.

An encyclopedia article offered Irving's (1974) final word on acclimatization. Here he defined acclimatization as "an adaptive change that is reversible when conditions return to their former condition." He treated the subject broadly, dealing with both plants and animals, poikilotherms and homeotherms, and changes involving adjustments to temperature, humidity, salinity, light, pressure, and certain environmental substances.

Though he did not use the terms, he touched on proximate and ultimate factors, noting that seasonal changes in day length can trigger such things as adjustments to temperature and preparation for migration.

In the book that serves as his valediction (Irving 1972), Larry drew on his extensive knowledge of Alaska and other high-latitude regions to describe the life of arctic birds and mammals. He discussed the characteristics of arctic environments, including their pronounced seasonality, and provided an overview of their history. His account of the birds and mammals included attention to indigenous populations of humans in both the Nearctic and Palearctic, tracing the migration of some of their ancestors into North America across the Bering land bridge. The physiological chapters of this book revisit the themes evident in his other reviews and symposium contributions, including the importance of supplementation of the modest physiological adjustments of indigenous arctic peoples to cold by appropriate protective clothing and shelter. Irving's book is an ecological as well as a physiological treatise devoting substantial attention to the factors that serve to maintain populations of arctic birds and mammals, including migration of many of the former and a few of the latter. I found its introduction revealing of his gratitude for the research opportunities he had been provided and his cognizance of the esthetic component of science. "I have enjoyed the scenes of arctic life, which I could not have seen without support by funds, supplies and transportation derived from a society that so generously sustains scientific research. I do not know what use the results may have, but for me the views of arctic life have been interesting, and I have a feeling that, like art, science is as valuable as it provides pleasurable interest" (Irving 1972, p. 3).

Laurence Irving, Advocate for Alaskan Research

The culmination of Larry Irving's scientific career occurred in Alaska, where, as noted (see "Professional Career"), he became an advocate for arctic and particularly Alaskan research. His enthusiasm was based on recognition of Alaska and other high-latitude regions as places where a combination of challenges posed to organisms by severe climatic conditions and pronounced seasonality create abundant opportunities for scientific, particularly biological, studies. Irving explained his advocacy for Alaskan research through several statements. "Nowhere, but in Alaska, can one find such favorable conditions as now exist for large returns in science from the investment of scientific labor. That condition largely is due to the fact that, with the aid of Alaskan perspectives, wise scientific conjectures may be made which permit experimentation to leap over incidental studies and penetrate to the center of scientific objectives. From vantage points less favorable for thinking, prolonged and often random preliminary investigations often are needed. But here, where there exist certain extreme conditions brought about by latitude, climate and geographical contrasts,

it is often possible to set out for remote scientific objectives by long flights of legitimate conjecture, rather than by hopping from one island of thought to another nearby" (Irving 1951b, pp. 113–114).

He further observed (Irving 1954, p. 1), "It is more obvious here in Alaska, but equally true in any situation, that intellectual progress moves through special opportunities for observation which open to the ready mind a view penetrating beyond common knowledge. If new views are to bring about distinct advances in human thought, they must be not only novel but they must be pertinent to large issues of timely and fundamental importance. For there are strategy and tactics in science whereby location and timing of the events observed can magnify or reduce the value of observations in bringing about the progress of knowledge and thinking."

"As we look with pleasure on the magnificent views which expanding scientific comprehension brings to us, we can think with modest satisfaction that we ordinary scientists are favored by time and our [Alaskan] location in gaining intellectual outlooks reserved in most places and times for the few whom genius or luck has enabled by abstraction to project new views. We can see that there are certainly strategic and tactical advantages of location and time in obtaining the advancement of knowledge" (Irving 1954, p. 5).

Laurence Irving, Comparative Physiologist

Laurence Irving was unusual for his time in the array of organisms that he studied; indeed, Field and Hall (1944, p. 75) noted that for him and his associates at Swarthmore, "Noah's Ark would have been an appropriate location in the space-time continuum." Moreover, he was part of what Somero and Suarez (2005, p. 26) have referred to in their memorial for Peter Hochachka as "the grand tradition of comparative physiologists such as Per Scholander, Laurence Irving, Knut Schmidt-Nielsen, and Kjell Johansen, whose approaches to their field exemplified the benefits and challenges of studying organisms in their natural settings, as well as in the more controlled confines of the laboratory." Field research in physiology was less common in the early phases of Larry Irving's career than it is now, and his enterprise in organizing the funding and logistics for remote efforts is impressive, particularly when one notes that many of his efforts occurred before the establishment of the National Institutes of Health and the National Science Foundation. His dedication to going where the problem required study (to practice what he referred to as "expeditionary physiology" [T. D. Simpson, "Dr. Laurence Irving"]) took his colleagues and him to marine laboratories such as Hopkins Marine Station; Marine Biological Laboratory; Marine Studios, Florida; the Biological Station at St. Andrews, New Brunswick, Canada; as well as to Mount Washington, New Hampshire; Barro Colorado Island, the Canal Zone; ARL at Barrow, Alaska; other arctic field sites; the Pribilof Islands; the Aleutian Islands; remote arctic villages;

and the Bering sea, aboard the research vessel *Alpha Helix*. Irving was also important to North American comparative physiology through his encouragement of young investigators and his assistance in the immigration of Per F. Scholander and the Schmidt-Nielsens to the United States.

In his pleasant and low-keyed way, Larry Irving had a significant role through his research and administrative activities in shaping environmentally oriented comparative physiology over several decades of the twentieth century. The Institute of Arctic Biology with its laboratories and various field sites, to which Irving contributed so much, is a leading embodiment of his philosophy of augmenting laboratory studies with field research. We can accord him no higher accolade than by recognizing that his work and approach, resulting in part from productive collaborations with Scholander, provided an important part of the foundation for the spectacular post–World War II expansion of functionally oriented ecological studies.

Acknowledgments

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