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IN MEMORIAM: JOHN THOMPSON EMLEN, JR., 1908–1997

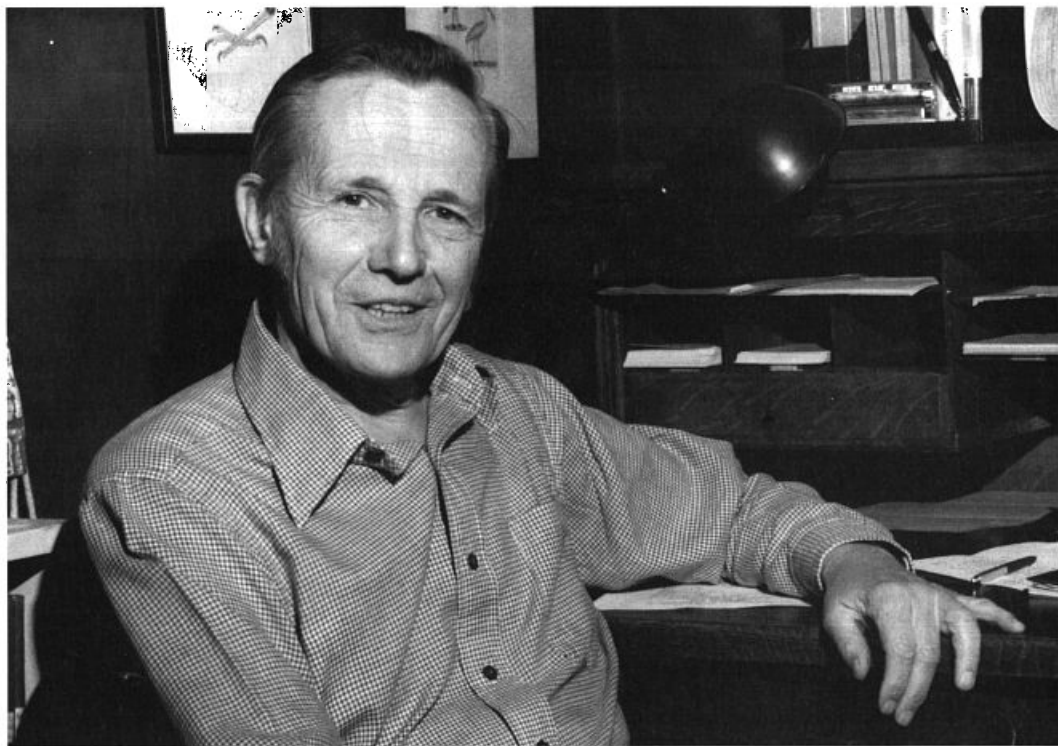
WESLEY E. LANYON,<sup>1</sup> STEPHEN T. EMLEN,<sup>2,4</sup> AND GORDON H. ORIAN<sup>3</sup>

<sup>1</sup>P.O. Box 531, Keene Valley, New York 12943, USA;

<sup>2</sup>Department of Neurobiology and Behavior, Mudd Hall, Cornell University, Ithaca, New York 14853, USA; and

<sup>3</sup>Department of Zoology, University of Washington, Seattle, Washington 98195, USA

“My fascination with birds started with a nature study teacher, Miss Trueblood, when I was eight or nine years old. My first notebook presented a systematic list with dates from 1919 when I was ten. It listed 51 species including such interesting identifications as hoot owl, poll parrot, wild duck, petrel, and crane. In 1920 I had 80 species listed, all of them recognizable and more or less correctly spelled. Two years later I was keeping notes on field identification marks and describing songs quite creditably with words and personally devised symbols.”



JOHN THOMPSON EMLEN, JR., 1908–1997

(On the occasion of his formal retirement from the University of Wisconsin in 1974. Photograph by Don Chandler.)

Thus started John Emlen's illustrious and fascinating career, as reminisced by him in his autobiography, *Adventure Is Where You Find It: Recollections Of A Twentieth Century American Naturalist* (published privately by the author in 1996). Soon to follow were a federal bird banding permit at age 15, a summer school ornithology course at Cornell University with Arthur A. Allen (while still in high school), two summers spent as a member of collecting expeditions to Haiti and Honduras for the Philadelphia Academy of Natural Sciences, and a stint as a volunteer during the summer of 1929 at the American Museum of Natural History in New York, receiving inspiration from the likes of Frank Chapman, James Chapin, Waldron deWitt Miller, and Robert Cushman Murphy. A return trip to Honduras in 1930, with an accidental encounter with the young Alexander Skutch, who was studying bird behavior, was a turning point in John's developing career. "Behavior was what had really intrigued me about birds all along, but to this point I had scarcely recognized it as a legitimate aspect of ornithology."

John Thompson Emlen, Jr. was born in Germantown, Pennsylvania, in 1908, the son of John Thompson Emlen and Mary Carpenter Jones. He was educated at Germantown Friends School, Haverford College (B.S. in 1931), and Cornell University (Ph.D. with Arthur A. Allen in 1934). Summers during his graduate school years were spent as a ranger naturalist in Glacier National Park. After brief jobs with Aldo Leopold at the University of Wisconsin and a three-month stint surveying waterfowl habitat in the Mississippi and Missouri River valleys for the Bureau of Biological Survey, he took a teaching position under Tracy Storer in the Zoology Department at the College of Agriculture in Davis, California.

During the next eight years he spent much time on the control of such avian pests as crows and blackbirds, but the populations of California Quail near the campus captured his special interest. Most influential at this point in his career was a visit from David Lack, during which the two men acquired data that later led to a joint paper on the nesting biology of the Tricolored Blackbird. There were regular trips to

Berkeley and visits with Joseph Grinnell, Alden Miller, and E. Raymond Hall.

It was during the eight years at Davis that John established his true identity as an ornithologist and naturalist. He wanted to be a player in a growing movement away from "the over-simplified descriptive biology that had characterized the old-fashioned natural histories," toward "a fresh new approach to field studies of wild creatures." But the exciting and rewarding times in Davis gave way to a time of discouragement and worry, fueled by the onset of World War II and the closing down of the Davis campus to house facilities for the U.S. Army Signal Corps.

John, a birthright member of the Society of Friends (Quakers), registered as a conscientious objector. This highly unpopular stand generated criticism from family, friends, and colleagues alike. To his great relief, he was assigned to an "alternate service" position at the Johns Hopkins School of Hygiene and Public Health, where he served as Rat Control Officer for the city of Baltimore. As ships from war-torn Europe docked in that city, rat populations boomed, posing the threat of rat-borne plague. John used his new position as a challenging opportunity to apply the ideas of habitat management he had learned from Aldo Leopold 10 years earlier, this time to fight a rat epidemic and to curb the spread of disease.

What John regarded as the "second half" of his life began with an invitation in 1946 to join the Zoology Department at the University of Wisconsin in Madison. He taught numerous classes in ornithology, mammalogy, population ecology, and animal behavior, and he led several generations of undergraduates on field trips throughout southern Wisconsin. Serving on numerous academic committees and a three-year term as Department Chairman convinced him that his real calling was in his creativity as a field researcher. A Fulbright Grant for research in Africa and a Guggenheim Scholarship for travel in Europe combined to create a sabbatical experience in 1953 to 1954 that was an effective relief from those administrative assignments. That year abroad ultimately led to friendships with distinguished European ornithologists and ethologists, including Niko Tinbergen, Konrad Lorenz, and Gustav Kramer.

Five years later (1959–1960), John returned to

<sup>4</sup> Address correspondence to this author. E-mail: ste1@cornell.edu

Africa, this time with graduate student George Schaller, to study mountain gorilla behavior. By the early 1960s, he was studying development of behavior in gull chicks on Kent Island in the Bay of Fundy and on islands off the coast of Newfoundland. Between 1962 and 1965, he and graduate student Richard Penny spent two field seasons conducting experiments on homing orientation of penguins in Antarctica. He also traveled through India and the Malay Peninsula, observing wildlife as well as the complex social and economic problems of those regions.

Symptoms of cardiac disease, first experienced during the penguin study at the South Pole, abruptly worsened in 1965 and necessitated a change in life style during the last 10 years of John's professional career at Wisconsin. He continued to teach animal behavior during the fall semesters but was obliged to go part time at the university because his doctors insisted that he migrate to warmer climates during the winter months. These enforced absences from campus required that he severely cut back his physical activity and that he work in more tropical locations. John used these "off" semesters to accompany some of his graduate students on their overseas projects (Gordon Stephenson studying rhesus monkeys in Japan, and Norman Owen-Smith studying white rhinos in South Africa), as well as to initiate new, more tropically based research projects that were compatible with his physical limitations. These included the development and testing of new avian census techniques and their employment in comparative studies of island, peninsular, and mainland avifaunal communities in Florida and the Bahamas as well as in Baja California and western Mexico.

In November 1974, the year of John's formal retirement from the University of Wisconsin, increasingly painful attacks of angina led to multiple coronary bypass surgery at the Stanford University Medical School. At the time, it was a relatively new procedure, one that had not been available when he first experienced heart trouble. The operation was a stunning success and, following surgery, John returned, in his own words, "to nearly full activity."

The entries in John's autobiography dated after his heart surgery read like a natural history tour brochure, and they fully support his contention of a full recovery: "Exploring Mexico's Prehistory and Natural History (1976)," "Africa

Again (1977)," "Hawaii (1978)," "South Atlantic Islands (1979)," "South Pacific (1980)," "Chihuahua's Copper Canyon (1981)," "Quetzals at Last: Costa Rica (1985)," "Churchill, Manitoba (1986)," and "Argentina (1989)," the latter including an ascent to 14,000 feet in the Andes at age 81!

When not busy traveling, collecting data, and observing animals in their natural state, in retirement John continued to analyze data and publish scientific papers. He remained active in field research until the late 1980s. In 1990, he began writing his autobiography, drawing heavily on the field journals that he had meticulously kept all of his life. Much of this autobiography has been excerpted in the journal of the Wisconsin Society for Ornithology (*Passenger Pigeon* 60:123-167, 60:203-250, and 61:7-69) and is available by writing to its editor, R. Tod Highsmith, at 702 Schiller Court, Madison, Wisconsin 53704. Thanks to this effort by the WSO, the highlights of John Emlen's life are available to anyone interested in learning more.

The research activities of John Emlen encompassed a truly remarkable variety of topics, on all of which he left his distinct and positive imprint. These include natural history, distribution and systematics, population dynamics, physiology, parasitology and pathology, community structure, research methods, and behavior. In all of these areas he always paid careful attention to the behavior of individual organisms. Animals never became simply numbers on which to perform statistical manipulations. He was as much interested in the differences among individuals as he was in their similarities.

As a researcher, John had a truly eclectic mind. He is not identified as the author of any major theories or conceptual advances in biology. Rather, he had the gift of sensing what was important in current controversies and knowing how to gather data to distinguish between competing hypotheses. He never stopped thinking as a scientist. His publications cover a period of more than 65 years, from 1926 to 1992. Through his diverse publications, several persistent themes characterize his research. Those that stand out most are summarized in the following five paragraphs.

John Emlen was a keen naturalist with a good sense of the importance of basic natural history information. He entered science through natural history, and he retained that interest

throughout his career. But he also recognized the importance of experimentation and performed some of the pioneering experiments in ethology and ecology. In 1941, he was already substituting contents of nests in colonies of Tricolored Blackbirds to determine how much the breeding cycle could be shortened or extended. In 1942, he was implanting hormone pellets in California Quail to manipulate their breeding behavior. In 1951, he was moving the nests of female Red-winged Blackbirds outside the territories of their males to determine if the males would enlarge their territorial boundaries to include the translocated nests. At about the same time he was helping design experiments to compare population dynamics in house mice permitted or denied the opportunity to emigrate.

Yet, John was always sensitive to the limitations of experiments and was alert to the possibility that experimental procedures themselves introduced artifacts that might mislead unwary investigators. He noted in his publications, for example, that the provisioning of food to mice at only one time each day might well explain the inability of dominant animals to prevent subordinates from gaining access to the food (antedating the idea of economic defendability in behavioral ecology). Moreover, experiments never became a substitute for good natural history observations, which for John provided clues as to which experiments were most important to conduct, and insights into the interpretation of the results.

Because of the broad range of his interests, John was always alert to the ways in which concepts and data from other fields might be useful to ornithologists and ethologists. He recognized the importance of ontogeny of behavior and performed insightful experiments on both altricial and precocial birds. Sensing that parasites, pathogens, and toxins might influence both behavior and population dynamics of organisms, he performed some pioneering experiments that helped explain the roles of stress and the responses of rats to poisoned baits. At a time when ethology was often accused, sometimes with justification, of neglecting proximate factors in favor of evolutionary explanations, he examined the implications of many proximate factors on behavior. His emphasis on individual differences helped him understand why population responses differed

from those that might be expected if one simply assumed that all individuals responded to perturbations in their environments in the same way.

While bringing insights from other disciplines to ethology and ornithology, John also used ethological concepts to approach problems in other fields. His ecological studies of peninsular effects and the structure of island avifaunas borrowed heavily on behavior as an explanatory variable. Some of this work foreshadowed the wide application of foraging theory to elucidate a variety of ecological problems.

Throughout his career, John understood clearly that field and laboratory data were no better than the methods employed to generate them. As a result, he had a sustained interest in research methods, making important contributions to methods of censusing animal populations as well as methods of estimating the limits of accuracy of field estimates of population densities.

John Emlen's association with the AOU began in 1925 when he joined at the age of 16. He became an Elective Member in 1941 and a Fellow in 1949. In 1973, he received the Union's prestigious Elliott Coues Award in honor and recognition of his pioneering research investigations on the behavior, ecology, and conservation of birds. He served as the Union's President from 1975 to 1976, but would have been so honored earlier had he not been burdened with heart disease. Additionally, he was a life member of the Association of Field Ornithologists and an Honorary Fellow of the Cooper Ornithological Society (elected President of the Northern Division in 1942). He served as President of both the Wilson Ornithological Society (1956–1957) and of the Wisconsin Society for Ornithology (1955–1956). John was intimately involved with the founding of the Animal Behavior Society and, in 1966, was honored by being one of 14 persons elected to the first group of Fellows for that society. In 1970, he was awarded an honorary doctorate by his undergraduate alma mater, Haverford College. The citation of the 1973 Coues Award reads: "To John T. Emlen, Jr., for pioneering investigations on the behavioral ecology of birds, including many original, critical, and significant studies of the living bird in its natural environment during the last forty years. By his early, exten-

sive, and systematic use of color-marking of birds as groups and as individuals, simple but effective field techniques and experiments, combined with census techniques and habitat measurements, he was one of the first investigators to establish modern approaches to the objective study of bird behavior in the field and to the scientific analysis of social organization and distribution of natural populations. He has made important and original contributions on the role of habitat and tradition in distribution, and to the understanding of orientation, behavioral ontogeny, and communication, as well as behavioral factors in population regulation. Not the least of his many contributions has been the guidance and inspiration he has so often given to others, including his many students, for scientific understanding and appreciation of the natural life of animals."

While a graduate student at Cornell, John had, in his words, "limited time" for girls. That is, limited until Virginia Merritt, daughter of Cornell physics professor Ernest Merritt and Bertha Sutermeister, transferred from Swarthmore College to Cornell for a degree in political science. John writes "I won't try to explain Jinny's charms and virtues, but they were devastating, and I soon recognized them as unsurpassable." He wooed her with early morning bird walks, awakening her discretely and quietly (without disturbing her sorority roommates) by tugging on a string that she had tied at its distal end around her big toe and then carefully draped out the window. The two were married on 25 June 1934 and remained devoted to each other for the next 63 years. Jinny was a constant and enthusiastic companion on most of John's travels.

John and Jinny Emlen successfully fledged three sons. All three agree they had the privilege of growing up in a family environment in which love, responsibility, and scientific curiosity were nurtured. They were encouraged to collect and catalog items from nature, and the "items" ranged from butterflies to owl pellets to abandoned bird nests. They were also encouraged to have pets. In various years, the back room of the Madison house was home to a family of prairie dogs, a Loggerhead Shrike, a raccoon named Scrapy, and a Great Horned Owl named Melvin. The dining room for many years was home to Harvey, a talking myna that entertained numerous visitors with his pontif-

ications, whistles, and imitations of such household sounds as the flushing of a toilet.

The Emlen family was able to accompany John on innumerable field trips, including the year's sabbatical to southern Africa in 1952-1953. For economic reasons, John frequently taught summer classes at biological field stations. In this way, his sons were able to spend formative summers in places such as the northern peninsula of Michigan, northern Minnesota, Jackson Hole in Wyoming, and Kent Island off the coast of Maine.

In all of their travels, John would teach his sons by asking questions rather than by answering them. In this way he instilled not only a love and respect for nature but also an avid curiosity about it. He drew attention to the things he observed by asking his sons what they thought was happening. The young, and perhaps naive, answers always led to new questions that stimulated additional discussion. And so, ever so subtly, he trained his children in the skills of formulating and answering scientific questions.

John Emlen's influence on his sons was considerable. All have pursued careers in the biological sciences. John Merritt Emlen is a senior biologist with the U.S. Geological Survey in Seattle, Washington. He has made important contributions to population biology and is author of two advanced textbooks on ecology. Stephen Thompson Emlen is the Jacob Gould Schurman professor of behavioral ecology at Cornell University. He has, perhaps, followed most closely in his father's footsteps through his field studies of avian behavior. James Woodruff Emlen chose a medical career in immunology (the "real" doctor, as Jinny often joked). He was, for many years, on the faculty of the University of Colorado medical school; he is now Vice President for Scientific Affairs at a biotechnology firm, InterMune, in Palo Alto, California.

One of John Emlen's greatest legacies is the group of graduate students he guided, mentored, and inspired at the University of Wisconsin, where he was affectionately and respectfully known as "Doc." Between 1949, when James Beer completed his thesis on muskrats, and 1974, when Ann Bleed finished her thesis on Red-winged Blackbirds, Patricia Moehlman defended hers on feral asses, and David Thompson completed his on Adelie Penguins, 39 students received their doctorates un-

der John's guidance. Many of them have gone on to become leaders in their disciplines throughout the world (21 are listed in *American Men and Women of Science*). Roughly half of his students studied birds, the others mammals. Among his ornithological doctoral students were Howard F. Young (1950), Arnold J. Petersen (1953), Richard R. Bond (1955), Wesley E. Lanyon (1955), Robert W. Nero (1955), John B. Millar (1960), Theodore D. Sargent (1963), Helmut T. Mueller (1963), Richard L. Penny (1963), John L. Kaspar (1963), Victor E. Rabinowitch (1965), Roger M. Evans (1966), John A. Wiens (1966), Don E. Miller (1966), Alfred E. Eynon (1968), David P. Barash (1970), Anthony F. Gramza (1970), Thomas C. Grubb (1971), Jerome McGahan (1972), Ann S. Bleed (1974), and David H. Thompson (1974). In addition, he mentored 22 master's students, for an astonishing total of 61 advanced degree students in 28 years of teaching! After his retirement in 1974, the University of Wisconsin established a scholarship fund in his name, to be awarded each year to a graduate student with outstanding potential for creativity in behavioral or ecological field research.

Whether or not John's graduate students were aware of his Quaker heritage, that upbringing demonstrated itself in many ways. A soft-spoken but enthusiastic, tolerant human being, he was a model of virtue and integrity. He took time for his students as individuals and cared about their families. In return, he not only attracted personal devotion from them, but also inspired them to carry on the tradition of positively affecting others as he had affected them. Many of Doc's students later acquired

teaching roles and graduate students of their own, and they became acutely aware of just how profound his influence on them had been when they began counseling students themselves. He was an effective stimulator who knew when to be supportive and when to be critical in his evaluations. His attention to detail, precision in expression, and avoidance of unnecessary verbiage often taught his students more about writing than had their English professors.

The last of John's overseas adventures, to Argentina in 1989, was followed by limited adventuring in the Madison area through 1994, when a heart attack terminated his almost daily walks along Picnic Point on the shore of Lake Mendota. John Emlen finally succumbed to his faltering heart on 8 November 1997, at the age of 88. Spanning the better part of the twentieth century, John Emlen's career was dominated by the theme of adventuring and an insatiable curiosity about the behavior of birds and mammals. Fortunately, his influence on that discipline will endure into the new millennium by virtue of his many scientific papers, his graduate students, and the myriad of other persons whose lives he influenced. Those of us who knew Doc were lucky to have been exposed to such a wonderful naturalist and teacher, and a truly gentle man. He loved the world around him and was able to convey that love and enthusiasm to those whose lives he touched. The final paragraph of his autobiography reads "By the time I reached the age of 80, in 1989, I could look back over a rich and rewarding life in which I had visited all of the world's six continents and a representative sample of its many islands. How lucky can a guy get?"