

Resolution of Respect

Frank A. Pitelka

1916–2003

Frank Alois Pitelka, Professor Emeritus of Zoology at the University of California at Berkeley, died on 10 October 2003 at his daughter's home in Altadena, California. His death, at age 87, was caused by complications from prostate cancer. Frank was a prominent player in the early discussions of concepts that underpin much of modern ecology. The scope of empirical studies conducted by Frank and his students was enormous and addressed such diverse topics as speciation, population regulation, bioenergetic constraints, territoriality, the niche concept, Arctic ecology, and the evolution of breeding systems. Frank was also a demanding, but supportive, mentor to the 37 Ph.Ds and 8 postdocs whom he trained at Berkeley.

Frank was born on 27 March 1916 and raised in Berwyn near Chicago. Both of his parents were born in Czechoslovakia, although they first met in Chicago. As a result, Frank learned to speak Czech at home and continued to do so at every opportunity throughout his life. Frank's father was a building contractor, and at his insistence, Frank studied the business curriculum at Morton High School and Junior College



in Cicero, a neighboring suburb of Chicago. (Frank's business training was reflected in the amazing speed of his typing and shorthand. His letters were swiftly drafted and, as a consequence, they retained the vividness of the original observations that prompted him to write.) In 1936, following his graduation from Junior College, Frank took a position as the secretary to one of the managers of the Electromotive Corporation, a subsidiary of General Electric. During this time, Frank studied on his own and passed the courses required for admission to the University of Illinois, where he majored in Chemistry and Zoology and graduated summa cum laude in 1939.

Frank started on the naturalist's path at an early age. In sixth grade one of his teachers, Miss Luckness, took the class on bird walks. He was so taken by this experience that he started watching birds on his own. In 1933, as his interests in the natural history of birds broadened, Frank learned of the Prairie

Club (a Midwestern version of the Sierra Club). He asked his teachers how he might attend club meetings. They arranged a meeting with Mrs. Nellie J. Baroody, a cultured woman who was active in circles devoted to natural history and conservation. She took a strong interest in Frank and invited him to participate in family activities. He accompanied her to public lectures and concerts as well as on field trips to prairies and the Lake Michigan dunes. It was through Mrs. Baroody that Frank was introduced to biologists at the Field Museum and the University of Chicago. Frank was always deeply grateful for Mrs. Baroody's sponsorship; she opened up a whole new world beyond his ethnic neighborhood, and introduced him to the music and cultivated lifestyle that he enjoyed throughout his life. Frank honored Mrs. Baroody by donating a student award in her name to the American Ornithologists' Union.

Frank started to develop his editorial skills at an early age by assisting Rudyard Boulton at the Field Museum with *Bird Lore*. He began publishing his observations on birds in 1935. He entered the University of Illinois in 1937, even though General Electric made him attractive offers to remain with the company. He was somewhat older, with more developed interests than the average undergraduate, and the ecologists on the faculty, S. Charles Kendeigh and Victor E. Shelford, treated him like a graduate student. He shared an office with two other noteworthy students of Kendeigh, Eugene Odum and Frank Bellrose. Frank had access to Kendeigh's library and read extensively on his own. He had a vivid memory of running across Charles Elton's 1927 book on animal ecology. He put everything aside and read into the night until he had finished. Elton had a profound influence on Frank's thinking—an influence that Frank put into context in 1957 and 1958 when he had an NSF senior fellowship to work with Elton's group at Oxford University.

Kendeigh and Shelford, who both received the Eminent Ecologist award, stimulated new interests in Frank and broadened his perspective. Shelford spent much of the 1920s and 1930s documenting the composition of North American biotic communities, including soft-bottom marine invertebrates, and with Frederic E. Clements, developed the biome concept. Kendeigh, who hired Frank as his research assistant,

emphasized studies of the distribution and abundance of birds, and had students in his ecology class draw maps of the distributions of biomes. No doubt as a result of these influences, some of Frank's early work included a review of the distribution of birds in relation to major biotic communities, including a map of North American biomes cited in textbooks, and the mapping of soft-bottom invertebrate communities in Tamales Bay, California. The biome map was Frank's senior thesis and brought an earlier map, by Shantz and Zon, up to date. Frank's map differed from the others in acknowledging that there are extensive regions that are best treated as "ecotones."

Frank moved to Berkeley, California, in 1940 with the intention of working on a Ph.D under Joseph Grinnell's direction. Grinnell died suddenly, however, of a heart attack just before Frank arrived. There followed an interlude during which Frank worked on a variety of topics, including studies on the rocky intertidal communities at Friday Harbor, Washington. Unfortunately, this work was never published.

It was at Berkeley that his romance with a fellow graduate student, Dorothy Riggs, blossomed and eventually led to a happy marriage with three children. Dorothy became a noted electron microscopist and held a research position in the Cancer Research Genetics Laboratory and an appointment as Adjunct Professor of Zoology until her retirement in 1984. She died 10 years later, but two sons, Louis and Vince, and a daughter, Kazi, have survived their parents, as have five grandchildren and two great-grandchildren.

As a student of Alden Miller, Frank was based in the Museum of Vertebrate Zoology where the Grinnellian tradition remained strong. During the 1940s and 1950s much emphasis at the Museum was focused on building collections for the study of geographic variation. Frank's doctoral research, for which he was awarded a Ph.D in 1946, took the form of a careful analysis of what can, and cannot, be learned from such data. In two monographs, one on shorebirds (dowitchers in the genus *Limnodromus*) and the other on the American jays (*Aphelocoma*), Frank developed hypotheses about how speciation may have proceeded within each of these two groups of closely related species. These monographs set new standards, broadened the conceptual scope of museum-based studies, and

continue to figure importantly in the analyses of biogeographic patterns, largely because of the extensive and carefully gathered data that they contain.

Frank also was an important pioneer in behavioral ecology. By producing superb papers that served as exemplars, he played an important role in defining the major questions and lines of approach in this discipline. Starting with his early work on territoriality and courtship in hummingbirds, he consistently placed behavior in an ecological context long before this was fashionable. Frank's extensive research on shorebirds (on both their breeding and wintering grounds) laid the groundwork for comparative analysis of behavior. This work was rich in details about foraging behavior, predator avoidance, interspecific interactions, and the timing of activities in a highly variable environment. In the late 1970s Frank started to collaborate with some of his graduate students on a long-term study of the Acorn Woodpecker at the Hastings Reservation in the Carmel Valley of California. This investigation, which continues, has yielded some of our earliest and most convincing demonstrations of cooperative breeding and kin selection.

In addition to his impact on avian ecology and ornithology in general, Frank made major contributions in other areas. Indeed, in some circles he is best known for his work on the interactions of small mammals with their food supply and predators. In the 1950s, in collaboration with Arnold Schultz, a plant ecologist and colleague at Berkeley, he developed the nutrient recovery hypothesis to explain population cycles of brown lemmings in the arctic tundra near Barrow, Alaska. Although subsequent work has not supported the details of this well-known hypothesis, particularly its emphasis on changes in quality of forage, it did inspire later research that documented the impact of small mammals on tundra and grassland vegetation. Furthermore, the interaction of lemmings with the quantity of available forage remains a favored explanation for lemming cycles. The studies by Frank and his students on the territorial and breeding responses of avian predators to fluctuations in lemming densities are still regularly cited. Concurrent studies in the Arctic included those of breeding populations of shorebirds, which began in the 1950s and blossomed in the 1970s, and studies of the demography of long-

spurs. Frank was clearly in his element during these 25 years of active field work in the Arctic, as anyone who had the good fortune to hear his enthusiastic daily reports of the latest discoveries can testify.

Because of his interest in population dynamics, Frank was an ardent participant in the debates that sprang up after 1954 about the regulation of populations. Frank was a champion of Lack's view that populations are most often held in check by density-dependent biotic factors. He was a speaker at the famous symposium at Cold Spring Harbor in 1957, which attracted leading ecologists from all over the world (e.g., H.G. Andrewartha, L. C. Birch, G. E. Hutchinson, and A. J. Nicholson) to weigh the relative importance of density-dependent and density-independent factors in limiting populations.

Frank's breadth of interests in systematics and evolution, in behavioral ecology, and in population and community ecology stemmed from his love of natural history and making first-hand observations in the field. He listened attentively to reports of new discoveries and immediately began musing about their significance for the grand scheme of evolutionary and ecological theory. His conversation and writing reflected his broad views, sometimes with considerable elaboration as he made eclectic references to relevant information, and always helped provide a more synthetic approach to the problem. It came as no surprise that after his retirement in 1985 he continued to contribute to the intellectual life of the Museum of Vertebrate Zoology and the Department of Integrative Biology. He was a regular attendee at the weekly meetings of the Behavioral Ecology Seminar, and the Museum Lunch. Ecolunch, which he founded in the 1960s, became a model for informal lunchtime meetings, a tradition that his former students spread throughout North America. In addition, he was often consulted for his historical perspective on the rise of ecology and evolutionary studies in the 20th century.

Frank's legacy to ecology lives on in his many graduate students and postdocs (listed below). His style of training research students was simple and highly effective; he continually asked questions that drew out significant insights. These cross-examinations took place in a variety of settings: hallway encounters where he stopped students to discuss a re-

cent journal article or a new bit of data, seminars and brown-bag lunches, where reasoning was expected to be more polished, and private lunches in one of Frank's favorite restaurants, where he reported his candid observations on personal issues that were holding back the work. Most of Frank's students developed a deep fondness for him because he cared about them as individuals, and his concern for them went far beyond that expected of graduate advisors. The closeness between Frank and his students was evident at his 70th and 80th birthdays, when many returned to Berkeley and helped him celebrate with all-day symposia (dubbed Pitelkafests). Frank's students also honored him by establishing the Frank A. Pitelka Award for Excellence in Research, which is awarded by the International Society for Behavioral Ecology.

Frank's extraordinary breadth of professional interests was also reflected in the variety of his personal interests. A social conversation with Frank likely would range from music (chamber music and opera were his passions), to art (he had an extraordinary collection of objets d'art), cuisine (he was known by sight at the best restaurants in the Bay Area), and gardening (he was an avid gardener, both in his yard and as a supporter of the University of California Botanical Garden in Strawberry Canyon).

Frank taught introductory and advanced ecology courses throughout his career. He also served in a variety of other capacities. For the University of California at Berkeley, he was Curator of Birds in the Museum of Vertebrate Zoology (1958–1963), Chairman of Zoology (1963–1966, 1969–1971), and Associate Director of the MVZ in charge of the Hastings Natural History Reservation (1985–1997). In addition, he edited three journals, *Ecology/Ecological Monographs*, *Condor*, and *Systematic Zoology*, and served on advisory panels for the National Science Foundation, the Atomic Energy Commission, the National Academy of Sciences, and the National Commission for UNESCO. Finally, he was the first Director of the Tundra Biome, a large-scale ecosystem research program in the early 1970s, supported by the National Science Foundation as a United States contribution to the International Biological Program.

Frank received many honors during his lifetime, including the Mercer Award and the Emi-

nent Ecologist Award of the Ecological Society of America, and the Brewster Medal of the American Ornithologists' Union. He was an elected fellow of the Arctic Institute of North America, the American Ornithologists' Union, the American Association for the Advancement of Science, the Animal Behavior Society, and the California Academy of Sciences, as well as an honorary member of the Cooper Ornithological Society. Because of his background, one of his proudest moments occurred in 1997 when he received an honorary doctorate in biological sciences from Masaryk University in Brno in the Czech Republic. In spite of all these honors for his scientific achievements, the one that he may have valued most was the Distinguished Teaching Award that he received from UC Berkeley in 1984. That award reflected the special relationships that he established with his students.

Finally, we would be remiss if we did not try to convey the ebullient personality that has led to Frank being described as "larger than life." Frank was prone to impatience, a trait that made driving with him an adventure. His imposing physiognomy and conversational style commanded attention at any gathering. This led some people to conclude that Frank was egotistical (or even imperious), when actually he was expressing his natural enthusiasm and playfulness. Frank's rich voice, hearty laugh, adept choice of words, and Darwinian enthusiasm for any new bit of information all contributed to his charm. He was generous with praise and took as much delight in the accomplishments of others as in his own. We shall miss him. Fortunately, he has left a legacy that will not soon be forgotten.

Acknowledgments

We thank Peter Connors, Harry Greene, Richard T. Holmes, Walter D. Koenig, Ronald L. Mumme, Louis F. Pitelka, and David W. Winkler, who answered our questions about what was going on during the periods when they were working closely with Frank.

Doctoral students and postdoctoral research associates of Frank A. Pitelka*

Ph.D students

Paul H. Baldwin, George O. Batzli, Donald L. Beaver, Jerram L. Brown, Henry E. Childs, Howard L. Cogswell, Thomas W. Custer, R. Glenn Ford, Arnthor Gardarsson, Russell S. Greenberg, Scott A. Hatch, S. B. Haven, Richard T. Holmes, Walter D. Koenig, Larry R. Lawlor, Stephen F. MacLean, William J. Maher, Michael P. Marsh, David A. Mullen, Ronald L. Mumme, J. Peterson Myers, Gordon H. Orians, Fernando I. Ortiz-Crespo, Oscar H. Paris, Stephen Pruett-Jones, Donald R. Roberts, Richard B. Root, Gregory M. Ruiz, Thomas B. Smith, Susan H. Thomas, William L. Thompson, J. Van Remsen, Nicolaas A. M. Verbeek, Stephen D. West, Pamela L. Williams, David W. Winkler, Jerry Wolff

Postdoctoral research associates

Tom J. Cade, Guy N. Cameron, Peter G. Connors, Janis L. Dickinson, Susan J. Hannon, Charles J. Krebs, Paul W. Sherman, Jeffrey R. Walters

In addition Frank was an important mentor to many ecologists who were never officially his students. We regret that we cannot include these people because the variety of connections makes it impossible to fairly say who was among them.

*This list was compiled from the names found in Pitelka 1993a (in the bibliography below) and in a newsletter of the International Society for Behavioral Ecology. The newsletter, dated May 1996, may be traced by contacting:

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Selected bibliography of the ecological publications of Frank A. Pitelka

This selection was drawn from a total of 129 papers in Frank's curriculum vitae. The list, which is in chronological order, was selected to illustrate how Frank's interests evolved and to record the breadth of his contributions.

Pitelka, F. A. 1950. Geographic variation and the species problem in the shore-bird genus *Limnodromus*. University of California Publications in Zoology **50**:1–108.

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Pitelka, F. A. 1958. Some aspects of the population structure in the short-term cycle of the brown lemming in northern Alaska. Cold Spring Harbor Symposia **XXII**:237–251.

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Pitelka, F. A., and A. Schultz. 1964. The nutrient-recovery hypothesis for arctic microtine cycles. Pages 55–68 in D. J. Crisp, editor. Grazing in terrestrial and marine environments. Blackwell Scientific Publications, Oxford, UK.

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MacLean, S. F., and F. A. Pitelka. 1971. Seasonal patterns of abundance of tundra arthropods near Barrow. Arctic **24**:19–40.

Pitelka, F. A., R. T. Holmes, and S. F. MacLean, Jr. 1974. Ecology and evolution of social organization in arctic sandpipers. *American Zoologist* **14**:185–204.

Custer, T. W., and F. A. Pitelka. 1977. Demographic features of a Lapland Longspur population near Barrow, Alaska. *Auk* **94**:505–525.

Pitelka, F. A., editor. 1979. Shorebirds in marine environments. *Studies in Avian Biology*, Number 2. Cooper Ornithological Society, Lawrence Kansas, USA.

Koenig, W. D., and F. A. Pitelka. 1979. Relatedness and inbreeding avoidance: counterplays in the communally nesting acorn woodpecker. *Science* **206**:1103–1105.

Koenig, W. D., and F. A. Pitelka. 1981. Ecological factors and kin selection in the evolution of cooperative breeding in birds. Pages 261–280 in R. D. Alexander and D. W. Tinkle, editors. *Natural selection and social behavior: recent research and new theory*. Chiron Press, New York, New York, USA.

Ford, R. G., and F. A. Pitelka. 1984. Resource limitation in populations of the California vole. *Ecology* **65**:122–136.

Mumme, R. L., W. D. Koenig, and F. A. Pitelka. 1988. Costs and benefits of joint nesting in the acorn

woodpecker. *American Naturalist* **131**:654–677.

Koenig, W. D., F. A. Pitelka, W. J. Carmen, R. L. Mumme, and M. T. Stanback. 1992. The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology* **67**:111–150.

Pitelka, F. A. 1993*a*. Academic family tree for Loye and Alden Miller. *Condor* **95**:1065–1067.

Pitelka, F. A., and G. O. Batzli. 1993*b*. Distribution, abundance and habitat use by lemmings on the north slope of Alaska. Pages 213–236 in N. C. Stenseth and R. Ims, editors. *The biology of lemmings*. The Linnean Society of London, England.

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