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CARL BARTON HUFFAKER

1914—1995

A Biographical Memoir by

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Carl Hubbard

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AT A TIME WHEN population ecologists and pest control specialists were arguing, sometimes passionately, about whether populations were regulated by biotic or physical factors (the density dependent/independent controversy) Carl B. Huffaker was carefully planning and meticulously conducting research to gain understanding of the population regulating mechanisms in various living systems and was rigorously analyzing his data and that of others. His conclusions, for which he was recognized as one of the leading population ecologists of his time, were the result of his strict adherence to research procedures of the highest caliber. His example as an imaginative, persistent, and demanding researcher is part of the legacy he left to all who were acquainted with him and his work.

Carl B. Huffaker was born in Monticello, Kentucky, on September 30, 1914. He completed his high school education at the Monticello High School in 1933. He attended the University of Tennessee, Knoxville, where he earned a B.A. degree (entomology) in 1938 and an M.S. degree (plant ecology) in 1939. He continued his graduate studies at Ohio State University, Columbus, earning his Ph.D. degree (entomology/ecology) in 1942. In 1936 he married Saralyn Knight of Monticello, Kentucky, who remained his wife for the rest of his life.

While still in college he spent the summers of 1937, 1938, and 1939 working on malaria control for the Malaria Studies Division of the Tennessee Valley Authority. During the 1940-41 academic year he was a graduate assistant (teaching) in zoology for Professor Dwight M. DeLong at Ohio State University.

From April 1941 to December 1943 he was an assistant entomologist at the University of Delaware Agricultural Experiment Station. A number of years later one of his more senior colleagues at the station commented on young Huffaker's abilities as a scientist: "Carl was amazing in his ability to analyze large amounts of complex experimental data and quickly reach accurate, sensible conclusions."

From December 1943 to January 1946 he was an entomologist for the Health and Sanitation Division of the U.S. Institute of Interamerican Affairs stationed in Bogotá, Colombia and then Santo Domingo (then Ciudad Trujillo), Dominican Republic. During this period he conducted field research on malaria in Colombia, Haiti, and the Dominican Republic.

In 1946 he joined the University of California as an assistant entomologist in the Department of Biological Control, Riverside. His first assignment was to lead, with James K. Holloway of the U. S. Department of Agriculture, the effort toward biological control of the Klamath weed. This European weed, also known as St. John's wort, *Hypericum perforatum*, had become in the 1940s a scourge on California range lands and threatened the grazing industry of northern California and other western states on some 2.25 million acres. A program of importation of several European species of insects that fed exclusively on the weed was started after reaching an agreement between the University of California and the U. S. Department of Agriculture's Bureau of Entomology and Plant Quarantine. The candidate species

had been tried in Australia, where the weed had been introduced in the 1880s. The insects had become established and provided some degree of control. Although it would have been easy, under normal conditions, to obtain the insects from Europe, the war made collection there impossible. After the necessary arrangements among the involved organizations, collaborators from the Australian Council for Scientific and Industrial Research collected the insects and prepared them for shipment, and the U.S. Army Transport Command took the responsibility to bring the material to California.

In California, at the Department of Biological Control in Albany, Carl Huffaker, Jim Holloway, and their collaborators took care of the imported material, reproduced the various species, and colonized them in the field. The colonized species were the leaf-eating beetles *Chrysolina quadrigemina* and *C. hyperici* and the root-borer beetle *Agrilus hyperici*. Eventually, a fourth species was colonized, the gallfly *Zeuxidiplosis giardi*. This program resulted in total and permanent control of Klamath weed in its area of distribution in the western states, where it is found at very low densities as a roadside plant in shady situations. The economic savings afforded by this project were estimated to be some $79 million as of 1984. The benefits continue to accrue.

Although the immediate economic benefits of this project are very significant, it has also contributed to the understanding of various aspects of the principles of biological control and population dynamics. Close, long-term quantitative studies by Huffaker and his collaborators on the consequences of this biological control project have led to improved understanding of the principles of biological control of plants and the ecological impact that phytophagous insects can have on succession and community (vegetational)

structure. In addition, this example provided insights into the nature of the whole complex of natural control of populations, involving both density-independent (e.g., weather and physical terrain) and density-related (dependent) factors such as regulating natural enemies or more direct competition.

In the context of basic science, this pioneering example was most important in showing the interactions of physical conditions and herbivores in determining the abundance and distribution of specific plant species and, consequently, the composition of vegetation.

Another long-term project led by Carl involved the biological control of puncture vine, a spiny-burred, toxic weed in wasteland, urban, and certain crop situations. Two weevils that interfere with the production of seeds significantly reduced the density of the weed in most of the affected areas. A significant ecological finding was that the destruction or prevention of seeding of about 45% was sufficient, apparently, to bring about the decline in the weed's population.

A student of population dynamics, especially of the interactions of factors determining density regulation, Carl Huffaker led field and laboratory work conducting "a series of experiments designed to shed light upon the fundamental nature of predator-prey interaction, in particular, and the interrelations of this coaction with other important parameters of population changes, in general." The field work involved the cyclamen mite, *Phytonemus pallidus*, a pest of strawberries, and two predatory mites in the genus *Amblyseius*, while the laboratory studies were done on the sixspotted mite, *Eotetranychus sexmaculatus*, and the predator *Metaseiulus occidentalis* on orange fruits. The cyclamen mite studies showed the principal role that predatory mites have in determining the pest population density. They also showed

that by purposely introducing the pest early in the cycle, the interaction between prey and predators was sustained and at a low density. This work pioneered the now common practice in certain areas of deliberate introduction of a pest species itself as a means of establishing quickly and perpetuating a solid biological control program. It also provided one of the clearest examples of the physical environment (density independent) and the density-dependent regulating agencies operating together to produce any given level of natural control. The laboratory work using orange ecosystems highlighted the contribution that heterogeneity of the environment can play in the balance of nature while not, however, entirely substituting for a basic density-dependent regulating mechanism.

Yet another project carried on under Carl Huffaker's leadership was the biological control of the olive scale. This insect was the major pest of California olives; it was also an important pest of many other deciduous fruit crops and ornamental shrubs and trees. The successful control of this pest was achieved by importation and colonization of two species of wasps that develop at the expense of the scale, killing it. In 1949 a search for natural enemies of the scale was started. One species was collected in various Mediterranean and Middle Eastern areas. The most promising material was collected in Iran and Iraq in 1952. This species became widely distributed in California. In 1957 a second species was found in Pakistan and was widely colonized throughout the state. During a period of some thirty years Carl and a group of collaborators implemented the program and carefully documented the biological and ecological interactions of the natural enemies with the pest and their economic impact on the olive industry. The result showed the effectiveness of natural enemies in regulating the density of their hosts, and strongly suggested that a

complex of natural enemies may complement each other and regulate the host population more effectively than one (the "best") acting alone. As for the economic impact, Carl estimated that the savings as of 1984 to the California olive industry were $15 million.

Biological control, as a tactic of pest control, in many cases involves the deliberate colonization of natural enemies into new areas. The procedence of these natural enemies may vary, and in any given area where biological control is implemented it may happen that several species, each one being a native of a different area, are colonized simultaneously or over a long period in the same area. Under these circumstances competition among some of the natural enemies may occur to the point that a species may be prevented from being established, or an already established species may be displaced by a newcomer. In other cases the species may complement each other, regulating the prey population at a lower level. The research on biological control of Klamath weed and of olive scale done by Carl shed significant light on this most important aspect of ecological interactions between living organisms.

In addition to his regular activities at the University of California, Professor Huffaker generously shared his scientific and administrative expertise by participating in a number of national and international organizations.

As a member of the Subcommittee on the Use and Management of Biological Resources of the U.S. National Committee of the International Biological Program, and as world coordinator of the IBP on biological control of spider mites, Professor Huffaker prepared, at the request of the National Science Foundation, a feasibility study for a long-term, nationwide, integrated pest control research program. The document he and his associates prepared was the basis for the project that eventually became widely known as "the

Huffaker project." This project, funded by the NSF and the Environmental Protection Agency, involved studies on six crop ecosystems, with nineteen land-grant universities and segments of the U.S. Department of Agriculture and U.S. Forest Service cooperating in the research. With an ecological approach to insect and mite pest control, the project has provided the expertise and methods for great reduction in the use of the more environmentally objectionable pesticides. As an example of the development of a stable program of pest control, the project serves as the prototype for integrated pest management programs worldwide.

Huffaker taught an undergraduate course in insect ecology for several years with Ray F. Smith and P. S. Messenger and a graduate course in insect population ecology. He also led numerous graduate seminars on biological control and insect ecology.

Under his guidance the International Center for Biological Control at the University of California, which he founded and directed, sponsored training programs, urban entomology research and education, and developed or sponsored books on integrated pest management and biological control. The center served also as a vehicle for other extramural-sponsored research, particularly crop ecosystem studies.

Huffaker was a longtime member of the International Organization for Biological Control, serving as its president from 1972 to 1976 and again from 1978 to 1980. He was president of the Entomological Society, member of the Executive Council of the Intersociety Consortium for Plant Protection, member of the Pesticide Advisory Board of the California Department of Food and Agriculture, and a member of the California Statewide Integrated Pest Management Project Organizing Committee. He served on a joint U.S./U.S.S.R. Integrated Pest Management Committee, which organized a reciprocal research and exchange effort. He

participated in global conferences and task forces of the Food and Agricultural Organization and the United Nations Environmental Program. His numerous services to educational and government agencies included consultations with and briefs to the Environmental Protection Agency, National Science Foundation, President's Council for Environmental Quality, Agricultural Research Policy Advisory Committee, and to a number of state and national investigative agencies. At the University of California he served on numerous academic and administrative committees.

Professor Huffaker's professional achievements were recognized in the following awards and special appointments:

Member of the National Academy of Sciences
The C. W. Woodworth Award for Outstanding Achievement in Entomology
Honorary fellow of the Royal Entomological Society of London
Scholar-in-residence, Rockefeller Foundation, Bellagio, Italy
Guggenheim fellow
Fellow of the American Association for the Advancement of Science
Fellow of the Franklin Institute
The Louis E. Levy Medal of the Franklin Institute, as well as its Journal Premium Award
Co-recipient of the Wolf Prize from the Wolf Foundation, Israel
Berkeley Citation

The results of Professor Huffaker's very productive scientific career are recorded in the more than 200 papers in numerous scientific journals and chapters in books. He was editor of several books on biological control and integrated pest management.

Although his scientific and academic activities demanded much of his time and energy, he gave ample love to his family. He was a most generous and gracious host to his numerous friends and acquaintances, and somehow he found the time for his hobby of many years: racing pigeons.

His physical and emotional strengths were put to a prolonged and sustained test after he learned of the gravity of his terminal ailment. His normal activities seemed to remain the same, and he continued being productive until very shortly before his death. He died quietly in his sleep the evening of October 10, 1995. He is survived by wife Saralyn, sons Ronald, Harry, and Thomas, and daughter Carolyn.

With Professor Carl B. Huffaker's death his family has lost a loving, guiding, supportive member; his friends, a generous, understanding, and unassuming fellow; his colleagues, a brilliant, inspiring, hard working, and fair partner; the world, a gentleman.

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