



## IN MEMORIAM

Joel E. Keizer  
Professor of Biological Sciences  
UC Davis  
1942 – 1999

Joel E. Keizer, a professor of biological sciences at UC Davis, died on May 16, 1999, after a battle with lung cancer. Keizer served the University of California for 28 years as a faculty member on UC Davis campus.

Joel was born August 31, 1942, in Oregon. He attended a high school in Beaverton, just outside of Portland, and graduated as president of his class in 1960. Aspiring to be a historian, he excelled at science. He entered Reed College in Portland as a chemistry major and then went to Princeton to study biochemistry, but soon returned back West to attend the University of Oregon and to marry Susan Swank, a classmate from Reed.

Joel started to work with Sidney Bernhard and published two papers in experimental biochemistry, but then, enamored by the power of theory, switched to theoretical chemistry. He received his Ph.D. degree in chemical physics in 1969 under the supervision of Terrell Hill, one of the founding fathers of modern theoretical biophysics, who pioneered studies on statistical thermodynamics, muscle contraction and polymer dynamics. Joel's thesis work was highly mathematical and appeared as papers in the *Journal of Statistical Physics* in 1970. The interplay between experiment and theory would characterize his work throughout his career. As a postdoctoral fellow at the Battelle Memorial Institute in Columbus, Ohio, from 1969 to 1971, Joel developed his theoretical skills and started to publish prolifically. He began his long association with UC Davis in 1971 in the chemistry department and rapidly rose in rank to full professor in 1978.

Throughout the 1970s, Joel's research interests focused on non-equilibrium thermodynamics. In more than 60 journal publications, he pioneered a quantitative description of non-equilibrium steady states and collaborated with experimentalists to test his theories. This stage of his scientific career culminated in a very successful monograph "Statistical Thermodynamics of Nonequilibrium Processes." In the following years, Joel's powerful intellect turned to mathematical modeling of cell biological phenomena (from 1993, he held an appointment as professor of biology). In the 1980s and 1990s, he developed novel mathematical models of insulin secretion, pancreatic beta-cell oscillations and intracellular calcium dynamics. His research resulted in a burst of papers published in prestigious journals such as the *Proceedings of the National Academy of Sciences (PNAS)*, *Biophysical Journal* and *American Journal of Physiology*. Joel's best known work, a model for insulin secretion published in *PNAS* in 1992, has been cited about 100 times and had a major impact on our understanding of this fundamental biomedical phenomenon. By the end of his life, Joel published more than 120 journal articles and book chapters.

Highly unusual for a theoretical biologist at the time, this modeling work was much appreciated and heavily cited by biologists, with whom Joel often collaborated producing joint experimental/theoretical papers that were at the onset of the modern quantitative revolution in biology. Respect and admiration for Joel's radically innovative modeling work and his insightful collaborations with experimental biologists translated into NSF

and NIH grants for his research. His last NIH grant was for theoretical research on calcium waves in frog eggs, which was highly unusual at the time, and started a trend that continues to today.

Joel's influence was not restricted to science: he was ahead of his time realizing that traditional individual pursuit of knowledge in academia has its limitations and that organized research units can spearhead overcoming key scientific challenges. In 1986 Joel established the Institute of Theoretical Dynamics (ITD) at UC Davis and was its director until his death. This interdisciplinary think tank brought together Davis faculty from different departments, visitors from around the world, and was especially instrumental as a training ground for young scientists and as a trampoline for their careers. Faculty, postdocs, and students worked together at the ITD in an atmosphere unconstrained by the boundaries imposed by traditional disciplines. The NSF selected the Institute for a research training grant on nonlinear dynamics in biology in 1997 that amounted to millions of dollars. Through this grant, Joel led an effort to mentor a broad group of interdisciplinary students and postdocs in the art of collaborative research. Many of these jump-started thriving careers through this training. Joel's influence was also crucial in organization of biophysical research at UCD. He helped to hire young biophysical UCD faculty and was a mentor, friend, and role model for them.

Joel was an outstanding teacher. Several generations of UCD students, to whom his door was always open, benefitted from his great lectures and interest and attention to their concerns. He was particularly noted for incisive and clear explanations of tricky biophysical theories and quantitative aspects of cell biological processes. By the end of his life, Joel had trained two dozen graduate students and postdocs. He was putting together notes for a book, which was finished after his death by his colleagues. This book, *Computational Cell Biology*, continues to serve as a source of knowledge and inspiration for hundreds of multidisciplinary students. Joel received many awards and honors in recognition of his achievements, including a prestigious John Simon Guggenheim Memorial fellowship in 1986-1987 and a fellowship of the American Association for the Advancement of Science in 1995. He was an invited speaker at many international meetings.

Joel was an affectionate man with love and compassion for his colleagues, family and friends. He often opened his home after seminars so that guests, colleagues, and students could continue discussing science in a convivial setting. He embraced all aspects of life with a particular passion for the outdoors. He regularly returned to his beloved Oregon Coast to spend time fishing, hiking and walking on the beach with his wife and children. At 56, Keizer was at the peak of his powers in research, teaching, and leading his colleagues when cancer overcame him. He is sorely missed by the scientific community and by his many friends who have been lucky to be bestowed with Joel's pervasive kindness and sense of optimism.

Angela Cheer  
Alex Mogilner  
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