RESOLUTIONS OF RESPECT

Fig. 1. Bill Schaffer with son Michael, 1987. Photo courtesy of Lars Folke Olsen.

Resolution of Respect

William M. Schaffer, 1945–2021

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Ecologist William (Bill) M. Schaffer died on 16 January 2021, in Tucson, Arizona, USA. He is survived by his wife, Tanya, and his children, Michael and Margaret. Bill was best known in ecology for his work on the theory of life history evolution and on nonlinear dynamics, but his contributions were much broader and his influence on the field substantial (Fig. 1).

Bill was an iconoclast. His work was brilliantly original, and he always aimed to ask fundamental questions. Most of his work was theoretical. While he used his excellent computational and coding skills (starting with Fortran) to solve difficult mathematical problems, he was skeptical of complex and elaborate computer models, always aiming to explain phenomena in terms of basic principles. He was excited about ideas and would express his enthusiasm to great effect. He had tremendous respect for rigorous and original thinking. Bill was the quintessential embodiment of the scholar who does not suffer fools gladly (at least those he considered fools), and he did not keep those opinions to himself. Yet, he could be lavishly kind and supportive as well. He was a difficult taskmaster, graduating only seven Ph.D. students, but those students became influential academic scholars themselves.

No matter what he was doing, Bill Schaffer always worked toward 100% success. When he made Peking duck, he had to have all the authentic ingredients, all the techniques, and two days of spare time. (The result was pure beauty.) Bill loved trains, particularly old-fashioned ones pulled by steam locomotives, and constructed an elegant and extensive model train layout to celebrate them. Bill Schaffer was simply a polymath with a drive to excel in whatever challenges he set upon.

While Bill lived in the west for his entire professional life and wore the cowboy boots to prove it, he had deep roots in the east. Born in Elizabeth, New Jersey, on 11 May 1945, he attended the Hackley School, in New York State, where he graduated as Valedictorian. As an undergraduate at Yale, Bill quickly became deeply immersed in research. He wrote a paper in the undergrad *Yale Scientific Magazine* on Charles Lyell and the origin of species (Schaffer 1965). He also wrote about male–male combat and morphology in the Caprinidae (sheep and goats) alone and with his advisor (Schaffer 1968, Reed and Schaffer 1972*a*, Schaffer and Reed 1972*b*). He earned his Bachelor's degree *Magna cum laude* with High Honors in Biology and was a member of Phi Beta Kappa.

His remarkable undergraduate record led to his acceptance as Robert MacArthur's Ph.D. student at Princeton, where he was an NSF Predoctoral Fellow and Princeton National Fellow. MacArthur's mentorship strongly influenced his thinking. His dissertation work focused on the theory of life history evolution, with a special focus on the evolution of semelparity in Atlantic salmon. During Bill's final year in grad school, MacArthur tragically passed away from cancer, after having an enormous effect on the field of ecology in his short career. Bill earned his Ph.D. in 1972 and went on to an Assistant Professorship at the University of Utah, but soon helped to launch the new Department of Ecology and Evolutionary Biology at the University of Arizona with Jim Brown, Michael Rosenzweig, Ron Pulliam, Bill Heed, Astrid Kodric-Brown, and other influential figures in ecology and evolution. He was a central contributor to building the department and to the development of modern thinking in evolutionary ecology.

Bill's work continued in life history theory during this time, doing fieldwork on *Agave* species and publishing highly influential theoretical work on the topic, with important papers in *The American Naturalist* (including the much-cited paper by Charnov and Schaffer 1973), *Evolution* (Schaffer and Tamarin 1973), and several in *Ecology*. His papers with Michael Rosenzweig, both on life history theory

(Schaffer and Rosenzweig 1977) and "Homage to the Red Queen," (Rosenzweig and Schaffer 1978, Schaffer and Rosenzweig 1978) have been important contributions to ecological thinking. Bill's papers on life history theory published in 1973–1979 (Charnov and Schaffer 1973, Schaffer 1974*a*,*b*, Schaffer and Elson 1975, Schaffer and Gadgil 1975, Schaffer 1977, Schaffer and Rosenzweig 1977, Gaines et al. 1979, Schaffer 1979*a*,*b*) have been cited almost 1,800 times and continue to be cited to the present. These papers' strong grounding in demographic theory made them both daunting to some readers (they are rather equation-rich) as well as influential in the longer run.

Observations made in the course of Bill's *Agave* work in the foothills of the mountains in southern Arizona led to a paper with a group of research assistants (Schaffer et al. 1979) on the cost of sociality in bees that is still cited. (He took his whole field crew out to see the premiere of the first *Star Wars* movie that summer.) Bill was a keen observer of nature, and he was particularly interested in watching birds. He loved the natural history of the southwestern United States. Indeed, while he was always mostly known as a theorist, his work after graduate school included papers on green turtles, *Agaves,* salmon, bees and other social insects, childhood diseases, and mammal and bird body size. With Richard Inouye, he also contributed an influential paper on the design of plant competition experiments (Inouye and Schaffer, 1981). He insisted that his graduate students have strong grounding in the biology and natural history of the organisms they worked with.

Bill had a deep-seated conviction that theory should be useful and not simply an exercise in mathematics. His later work on life histories reflected this. In Schaffer (1983), he showed that reproductive effort (RE), a central notion of the theory that he had worked hard to develop (though it was first suggested by Williams (1966)), could not really do the job asked of it. The problem was not simply that RE was defined vaguely and, therefore, used in different ways by different researchers. It was that RE was a static measure: The fraction of total resources available to individuals that was devoted to reproduction. A given value of this fraction, he showed, does not uniquely determine a life history. Thus, he devoted several papers (Schaffer et al. 1982, Schaffer 1983) to adapting optimal control theory (a technique of dynamic optimization) to life history problems. This approach is not much used today (which may be a shortcoming of our science) but Bill's insight here remains valuable: The problem is a dynamic one that must capture some detail of the organism's life history.

Bill's dedication to full explanations helps us to understand at least part of the trajectory of his career. By the early 1980s, Bill had become quite concerned about a deep problem: We typically study one or a handful of populations at a time, but there are many more populations interacting with these. This is true of both empirical and theoretical studies. For example, when we model the growth of a single population, we can analyze the model and ask at what point density dependence becomes important, or the population dynamics change qualitatively. But when we study the growth of a real population, its growth depends on many things, including many interactions with other species. The quantity we estimate empirically as a growth rate in that population is not the same thing as the quantity in our single-species model!

Bill's concern with inference about high-dimensional systems from study of low-dimensional subsets led him to a major change in his research program. As is often the case in ecological field studies, he had encountered results in his work with *Agaves* and bees that were entirely unexpected: ants were draining the flowers of nectar overnight, so that hypotheses about bee behavior could not be directly tested. It was easy enough to exclude the ants, but Bill became interested in a more general question: How many variables must one really account for to understand ecological processes? This problem first led Bill to write a paper on "ecological abstractions" (Schaffer 1981). Here, he analyzed the problem for community ecology and asked questions about when the "abstracted" system (the one we are studying) can give qualitatively correct answers about the complete, higher-dimensional system. For questions like community stability, the paper showed, the general answer is that it depends on the time scale of population growth for the species modeled as compared with the time scale for those omitted. Bill suggested experiments in this paper that would allow one to estimate the importance of the omitted interactions. This paper is still cited, and while community matrices are little studied today, the general conceptual approach he brought to this paper still has much to offer for ecological thinking. But for Bill, the result was no less than a dagger plunged into the fabric of his scientific world. He had shown that reducing the number of variables in a theoretical system can render the conclusions invalid. And since all theoretical studies of ecological systems had to work with fewer variables than were truly present, such studies may often produce unreliable answers. Ouch! It was a result that Bill could not ignore. It made him question much of ecology as it stood at the time, and it forced him to reorient his research.

A major revelation for Bill came from dynamical systems theory. The Dutch mathematician Floris Takens (1981) had proven a theorem showing that, by using appropriate lags, one could use even a one-dimensional time series to qualitatively reconstruct the dynamics of the complete, higher-dimensional, system. Bill repurposed some of the same mathematical tools and techniques that he had learned as an ecologist. He used them to focus on forecasting the dynamics of human diseases like measles, and he did it with considerable success. Using these tools and Takens' approach, Bill found evidence that the dynamics of the famous lynx population data set, based on fur returns, were chaotic, and so were the dynamics of measles in human populations.

In James Gleick's (1988) popular book *Chaos: Making a New Science*, the author describes Bill's epiphany about chaos in the early 1980s:

> *He happened upon a reprint about chemical chaos and he felt that the authors had experienced exactly his problem: The impossibility of monitoring dozens of fluctuating reaction products in a vessel matched the impossibility of monitoring dozens of species in the Arizona mountains. Yet, they had succeeded where he had failed. He read about reconstructing phase space. He finally read Lorenz, and Yorke, and others. The University of Arizona sponsored a lecture series on "Order in Chaos." Harry Swinney came, and Swinney knew how to talk about experiments. When he explained chemical chaos, displaying a transparency of a strange attractor, and said "That's real data," a chill ran up Schaffer's spine.*
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> *"All of a sudden I knew that was my destiny," Schaffer said. He had a sabbatical year coming. He withdrew his application for National Science Foundation money and applied for a Guggenheim Fellowship. Up in the mountains, he knew, the ants changed with the season. Bees hovered and darted in a dynamical buzz. Clouds skidded across the sky. He could not work the old way anymore.*

Bill was hooked, and he focused on the importance of nonlinear dynamics for ecology. Bill was awarded a Fellowship by the John Simon Guggenheim Foundation to study nonlinear dynamics in ecology. But while ecology was one of the disciplines in which chaotic dynamics had first been investigated (notably in May (1974) and Hassell et al. (1976)), ecologists were not quick to embrace either the UK group's suggestion of the importance of chaos, or Bill's suggestion a few years later. In their 1986 TREE paper, Bill and his then-student Mark Kot argued that chaotic dynamics were likely widespread in ecology, and that this might necessitate a fundamental reappraisal of many ideas in population and community ecology (Schaffer and Kot 1986). Ecologists either ignored this work, or they were less than convinced. A review by Hastings et al. (1993) suggested that it may be more challenging to make a convincing case for chaos from ecological time series data than Bill had suggested. Not impossible, but certainly no slam-dunk, partly because most ecological data sets are too small and too short. Nevertheless, examples have accumulated over time that provide evidence for chaos in at least some ecological systems (e.g. Costantino et al. 1997, Benincà et al. 2015). It is unclear whether it is as widespread as Bill argued, but determining that may require datasets that are longer than many ecological datasets or are specifically designed to discern the nature of the underlying dynamics.

Be that as it may, the "hunt for chaos" that preoccupied so many theorists during this period, and in which Bill played such a provocative role, yielded many insights of lasting value, and proved a necessary prelude to the current synthesis, which views population dynamics as the interplay of deterministic and stochastic forces. Bill was particularly proud of his deep insights into the mathematical structures unifying models of population cycles in disparate biological systems, from boreal mammals to forest insects to infectious diseases to biochemical kinetics (King and Schaffer 1999, King and Schaffer 2001, Schaffer et al. 2001). He played an important role, too, in speeding the synthesis along, for example by making space in his laboratory to Robert F. Costantino, the experimentalist whose flour beetles provided ecologists with their first dose of demonstrably chaotic dynamics, albeit one that came from a bottle. In addition, his Dynamical Software (Schaffer and Truty, 1987), a suite of DOS-based programs (with cutting-edge graphics for their time), made many of the analyses available to ecologists and medical scientists with limited programming skills.

Bill moved on to work on nonlinear dynamics in disease systems with his Danish collaborator Lars Olsen for many years (Olsen et al. 1988, Olsen and Schaffer 1990). In 1985, Lars was preparing a review on “Chaos in Biological Systems” and came across the wonderful paper by Bill and Mark Kot on chaos in measles epidemics (Schaffer and Kot 1985). He immediately wrote to Bill for permission to reproduce some of their graphs in the review, and he invited him to give a talk at a conference, *Chaos in Biology*, to be held in Wales, U.K., the following year and to come and visit in Odense before the conference. This was the first of Bill's many trips to Denmark. After the conference, Bill invited Lars to come and work in his laboratory in the fall semester of 1987.

Lars recalls many visits to each other's laboratories and that they had so much fun, scientifically and socially, although they didn't enjoy each other's jokes very much. Over the years, they had numerous fruitful scientific discussions. When at times, they disagreed as to how to approach and solve a scientific problem, they always found a compromise. During a visit to Odense in 1994, Bill met a Russian scientist, Tatiana (Tanya) Bronnikova, who was visiting the laboratory there. Bill and his first wife, Valentine, had divorced by that time. After Bill returned to Arizona, he invited Tanya to visit him in Tucson. About a year later they married. They were often seen walking on the University of Arizona campus together holding hands, and they collaborated on many scientific papers (Bronnikova et al. 1995, 1996, 1998, 2001, Hauser et al. 1997, Schaffer et al. 2001*a*,*b*, Olsen et al. 2002, Schaffer and Bronnikova 2007*a*,*b*, 2009, 2011, 2012).

Bill loved his family more than anything else. Tanya and his children Michael and Maggie (Margaret, named after Margaret Thatcher) were his highest priority. Bill could not accept the widely varying diagnoses of Michael's medical problems, and he and Tanya dug deeply into the medical literature until they found a resolution, and wound up publishing a paper on this complex medical problem (Mukaetova-Ladinska et al. 2012). He once remained in a hospital with his son Michael when Michael suffered a frightening, life-threatening episode; his doctors gave up on Michael, but his father did not. Improbably, Michael survived. In this sphere, too, Bill did everything one hundred percent.

Bill was a superb teacher, and he brought to his teaching the same commitment as to his research. One of his long-lasting contributions to the field of ecology was his cohort of Ph.D. students: Hedley Bond, Deborah Goldberg, Jessica Gurevitch, Mark Kot, Gordon Fox, Bruce Kendall, and Aaron King. His demand for 100% rigor may well be the reason those of his students who finished have been so successful. They were all profoundly influenced by Bill, who always pushed them to think more deeply and critically; together, they have published hundreds of papers, textbooks and other influential work that has been cited tens of thousands of times. He allowed them to make mistakes, and to learn from them. He scared the hell out of us on occasion. His course on ecological theory influenced generations of graduate students at the University of Arizona.

Bill sought the same degree of intellectual rigor in the many undergraduates he taught. In more recent years, Bill taught the ecology and evolution portion of an undergraduate honors section of introductory biology. He put a tremendous effort into this course and took great pride in the students' success. Once, he came into the laboratory before class wearing a tweed jacket and nice slacks, and when a graduate student commented on his natty attire, he said with a deadpan expression that today he was going to teach Fisher's Fundamental Theory of Natural Selection. The combination of the sports jacket and ever-present pipe from his Ivy League formative years, with the cowboy boots and bolo tie (if any tie was worn) were Bill Schaffer from top to toe.

Earlier in his career, he was known for undergraduate teaching that could be inspirational, if intimidating. In 1975, he substituted in Bill Heed's course "Principles of Evolution" when Professor Heed was on leave at NSF. Schaffer developed a remarkable, entirely novel, and ambitious syllabus. For the first third of the semester, they read Greene's (1959) history of evolutionary thought before Charles Darwin. All but 35 of the students immediately dropped the course. This was followed by the era of Charles Darwin, with prolific studies of fossils. When the final third of the course came, Bill filled the chalkboard with equations modeling population genetics. All but seven students dropped. Of the seven, one failed. He complained. Bill held his ground. Poor Bill Heed; after a year, he returned and had to rebuild the enrollment of the course. But the department head always felt that Bill Schaffer's devotion to his students and subject matter was all too rare.

Bill was well known as a guy who wasn't easy to get along with. He was blunt. He could have been more diplomatic, but he took ideas seriously and argued for what he believed, and he was not afraid or unwilling to be shown to be wrong. He loved classical music, especially opera and particularly Wagner's

Ring Cycle. He greatly enjoyed being a contrarian, as he once admitted to a graduate student, and he was an outspoken political conservative in an ocean of liberal and progressive thinking.

Bill Schaffer was a stellar scientist in many ways. He was motivated much more strongly by ideas and by curiosity about the world around him than by the metrics so beloved by university administrators. Yes, he wanted grant funding and publications and even accolades, but he wanted to understand the world even more. He made big contributions to science, and he will be much missed.

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