In memoriam Eldridge S. Adams (1957–2019)

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Eldridge Stevens Adams was a brilliant insect behavioral ecologist whose research focused on social behavior as a mechanism of ecological interaction, animal contests, social insect genetics, and the organization of group action in diverse taxa. His work represents an innovative and important integration of theory, modeling, and field study. His quick intellect, experimental research skills, and dedication to undergraduate and graduate education have advanced behavioral and ecological science, and left indelible marks on those who had the pleasure of knowing him (Fig. 1).

Eldridge was born on September 11, 1957 in California's San Fernando Valley, where he developed a love for science, nature, and insects—especially ants. From an early age, it was clear he was gifted intellectually and would pursue a career in the life sciences. In 1976, he was admitted to Harvard, the social insect Mecca, where he began to develop as a behavioral ecologist in the company of Edward O. Wilson, Bert Hölldobler, their nests of students, and the world's best ant collection. He completed an Honor's Thesis under Hölldobler, working closely with JT, on chemical interference competition in *Monomorium* ants. This work was published in *Oecologia*, marking Eldridge's first scientific paper. He graduated *summa cum laude* in spring 1979, completed research over the summer, then entered a doctoral program in Roy Caldwell's lab at the University of California, Berkeley. He was awarded a three-year National Science Foundation Graduate Research Fellowship in his first year.

Eldridge planned to study the behavior of stomatopod crustaceans in Panama, but remained inspired by social insects, especially their recruitment and territorial behaviors. During his second year at Berkeley, an award to support a “side project” to study *Azteca* ants in Panamanian mangrove communities provided his first opportunity to work in the tropics, where he became interested in termites. While working on stomatopods and *Azteca*, he published two papers with Sally Levings on mangrove *Nasutitermes*.

After receiving his Ph.D. in 1987, Eldridge secured funding for his three postdoctoral positions, the first two at the Smithsonian Tropical Research Institute (STRI) with Mary Jane West Eberhard, allowing him to extend his research in Panama. His third postdoc resulted from a proposal he wrote with WT as principle investigator, leading to a three-year NSF award on fire ant territoriality and population biology, and establishing a close, long-term relationship between the two researchers. Eldridge was very soon offered an Assistant Professorship at the University of Rochester, where he continued work on fire ant territoriality. In 1992, he was awarded a prestigious five-year Packard Foundation Fellowship and honored as the James P. Wilmot Distinguished Assistant Professor. While Eldridge's career flourished at Rochester, the biomedical and molecular biology focus of his department was not satisfying, and Eldridge sought a position in a department where he would have more colleagues in organismal biology. In 1997, he joined the

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Fig. 1 Eldridge Adams in mangrove forest, east coast of Panama, when a graduate student (left); in the field in Massachusetts

Department of Ecology and Evolutionary Biology at the University of Connecticut, where he was surrounded by a number of familiar faces and friends from his time at UC Berkeley that included Robert Colwell, who served on Eldridge's Ph.D. committee. At UConn, he broadened his research to encompass termites, developed molecular markers for assessing kinship, and expanded his statistical and programming skills.

Eldridge's studies integrated population dynamics and genetics, social behavior, evolution, and invasiveness, and he became a preeminent authority on territorial interactions in social insects. Because aspects of ant and termite conflicts are analogous to human warfare—recruitment, combat escalation, and attrition—he was funded by the US Army Research Office to test military theory such as Lancaster's Laws of military engagements, using ants as a model. He also studied how diverse social animals self-organize, and became especially interested in cooperation, including herding behavior in dogs.

Eldridge's work, and that of his students, was anchored in theory, statistical modelling, and broad knowledge of relevant literature. He was one of the most quantitatively minded of his cohort of behavioral ecologists, selflessly making time to teach statistics to lab mates and others. He began using computers at a time when punch cards were required. An early programmer, he began writing his own code, and at UConn was among the first biology faculty members to harness Bayesian inference and R programming for computing and graphics. He developed new courses to help graduate students (and fellow faculty) employ these and other newly emerging statistical tools and methodologies.

Eldridge was a gifted experimentalist with unusual strength in integrating ideas and methods from disparate disciplines into his studies. He innovatively connected game theory, military strategy, and plant demography with studies of social insect interactions. He was the first or sole author on more than half of his 52 publications that appeared equally in behavioral and ecological journals. His work was published in top-tier journals, including an article in *Science* on animal

cooperation and a sole-author paper on heritable nestmate pheromones in the *Proceedings of the National Academy of Science*. Seven of his papers appeared in *Behavioral Ecology and Sociobiology*, more than any other journal. His most highly cited paper is his 2001 *Annual Review of Ecology and Systematics* contribution on territory size and shape.

Eldridge was an excellent mentor and teacher, who enjoyed consistently outstanding evaluations from undergraduate and graduate students, and appreciation from faculty colleagues. His social insect course was life-changing for many, with several students pursuing careers in entomology and behavioral ecology. While his staple was undergraduate ecology, his passion was for graduate courses and seminars in population and community ecology. Three of these were on biostatistics and Bayesian inference. He created and led a formative graduate seminar on teaching pedagogy. In 2016, his many significant contributions to graduate education were recognized with the prestigious Faculty Excellence in Graduate Teaching Award.

Eldridge's had a lightning wit and delightful capacity for encapsulating complex ideas into pithy aphorisms. Here are three. On NSF's granting process of obliging resubmission of virtually the same proposal two or three times to secure funding, "I can't figure out if it is a meritocracy or a queue." Discussing teaching, he quipped, "Students are the only consumers that want less for their money." Living in Rochester and conducting field research in Florida, he noted "You know, by spending my winters in Rochester and my summers in Tallahassee, I get to experience the perfect average yearly temperature." He had a special talent for impersonation; his renderings were playful with spot-on mannerisms, phraseology, and accents.

We regard Eldridge as one of our most intellectually gifted colleagues: a widely read polymath and wry conversationalist, who seemed to have studied in-depth on virtually any topic that might surface in conversation at a professional meeting or the "Wee Nip" single-malt scotch get-togethers that he attended. At the same time, he was a quiet, private person, who would prefer to read and cogitate within, rather than offer

uninformed opinion. He maintained an extensive library rich in classic literature, world history, collections of art and photography, a diverse array of natural history guides, and, of course, important works in ecology and behavioral biology. His film and music collections were equally eclectic, the latter a throng of acclaimed world music, opera, jazz, and rock. JT sentimentally remembers Eldridge's enthusiastic review of a Devo concert. For several years, he led a natural history club for biology students. He recently became fond of travel and world culture, cycling, and theater; and was a steadfast supporter of the acting efforts of his lifetime love and wife, Jan.

Eldridge Adams remained an active member of Ecology and Evolutionary Biology at UConn until the summer of 2018. He died November 2, 2019. We deeply lament the premature loss of a brilliant mind, deep and creative thinker, exceptional experimentalist, award-winning teacher and dedicated mentor, gifted statistician, and witty, treasured friend and colleague. His passing diminishes each of us, as well as the fields of behavioral ecology and insect sociobiology.

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