Marjorie A. Asmussen 1949–2004

John C Avise

On January 19, 2004, Marjorie Asmussen died suddenly when the bicycle she was riding was struck from behind by a pickup truck on a country road near Athens, Georgia. She was 54 years old. Marjorie had a zest for life that few of us can match. In her professional life, this enthusiasm was evidenced by her devotion, both in research and teaching, to vitalizing the oft-abstruse field of mathematical population genetics. In her personal life, Marjorie's irrepressible spirit was reflected in the unbridled joy and physical exuberance that she brought to almost every task. Marjorie died instantly, unexpectedly, while doing exactly what she loved on a warm sunny day in the normally gentle Athens countryside. She is survived by two daughters (Meg and Jenny), both in graduate school.

Marjorie was a mathematical geneticist *par excellence*. She received her A.B. degree in mathematics from Occidental College in 1971, graduating *summa cum laude*, before going on to Stanford University where she earned two M.S. degrees (in mathematics and statistics) and a Ph.D. in mathematics (working with Marcus Feldman). In 1976, she moved to the University of Georgia, where she was my friend and colleague for 28 years, first in the Zoology Department and later in the Department of Genetics. During that time we collaborated on several research projects, shared advising duties for some Ph.D. students, worked together on many committees (Marjorie was always appreciated for her conscientiousness and energy in community tasks) and enjoyed our weekly lunches with several other members of our population genetics faculty. At the Friday lunch before her death, we reminded an overworked Marjorie that Monday was the Martin Luther King Jr. holiday, to which she responded, "Oh, good. Maybe I'll have enough time for some bike-riding this weekend after all."

Marjorie's research centered on the use of mathematics to develop theoretical frameworks for population genetics and ecology. By deriving formal mathematical models and then analyzing them using combinations of analytical and numerical techniques, she sought to provide conceptual backdrops for interpreting the kinds of empirical data on genetic polymorphisms often generated in the fields of molecular ecology and population genetics. A representative sample of the diverse topics that she addressed indicates the breadth of Marjorie's research interests: frequency-dependent selection as an evolutionary force for protecting genetic polymorphism, coevolution of gamete-recognition loci, detection and decomposition of gene flow into its underlying components, maintenance of genetic variation by regular and chaotic cycling in gene frequencies, evolution of organelle inheritance patterns, and applications of genotypic data in human genetic counseling. She is perhaps best known for her development and promotion of 'cytonuclear disequilibrium statistics' that codify and facilitate interpretation of nonrandom associations between alleles at genes in the nucleus and cytoplasm. Almost single-handedly, Marjorie's research group developed a large body of theory regarding cytonuclear genotypic associations, and this theoretical construct has been very useful for analyzing population-genetic data for haploid loci in cell organelles (*e.g.*, mitochondria and chloroplasts) jointly with those for diploid genes in cell nuclei. Marjorie published more than 60 peer-reviewed articles during her too-short career and delivered more than 80 invited seminars. In 2002, she was formally recognized for her scientific accomplishments by election into the American Association for the Advancement of Science.

> Marjorie had that all-too-rare ability to see biological phenomena through the eyes of equations and mathematical proofs, but many in her remarkably wide circle of friends will remember Marjorie more for her effervescent attitude and high-spirited approach to life than for her sterling science.

Two personal anecdotes might give some glimpse into the workings of Marjorie's mind and heart. In 1987, Marjorie published, with Jonathan Arnold and me, her seminal paper (the first in a long series) that defined and described various properties of disequilibrium statistics for associations between nuclear and cytoplasmic genotypes. As we worked closely together for several weeks drafting the text and tables, it struck me (for the first time, I recall) that different people's minds genuinely can and do work in different ways. To Marjorie, 'biological intuition' meant relatively little unless it could be mathematically formalized, whereas for a nonmathematical biologist like me, any biological 'insight' must (sadly) remain forever at the intuitive level at best. To her credit, in an intellectual context she demanded no less of her students and postdocs.

A second personal anecdote concerns Marjorie's collaboration with my lab to analyze genetic patterns in hybrid zones. Marjorie's statistical models as applied to our cytonuclear data had helped, for example, to uncover asymmetric mating patterns in a hybrid population of treefrogs, but Marjorie had never actually seen the living animals. One weekend, for the fun of it, Marjorie accompanied my ornithology class on a field trip to the Georgia coast, where we happened upon a green treefrog that I caught and handed to Marjorie. She literally squealed with unbridled delight to think that the gorgeous creature about which she had written was actually nestled there in her palm. Marjorie had a brilliant mathematical mind, but in her heart she was also a hopeless romantic in her love of the great outdoors and its inhabitants. Her incandescence was extinguished far too soon, but its lasting glow will shine on in our minds and hearts.

John Avise is in the Department of Genetics, University of Georgia, Athens, Georgia, 30602. e-mail: avise@uga.edu