"A deeper understanding" was one of James Crow's favorite phrases when he lectured. It is also a good way to sum up the gift he leaves to science. His field was genetics, especially population genetics. He was known and revered as much for inspiring generations of students and colleagues as for his numerous original contributions to the field.

I was one of the thousands of students whose indelible first impression of James Crow came while attending his undergraduate lectures. It seemed he was every student's favorite professor. He would begin by telling the class that genetics was a difficult subject, then proceed to convince us of the opposite. His lectures were models of clarity spiced with enough humor to keep the attention of even the most jaded students. One measure of how thoroughly he captured the students' attention was the
length of time he could hold a silence in front of hundreds of students. I recall when a student asked him a particularly thought-provoking question during a lecture, Crow simply smiled and began to think through the problem. The large class was dead silent as Crow unsel{consciously stood, paced or stroked his chin for a very long time. When he finally spoke the answer was dazzlingly clear and left us all with a new depth of understanding.

Crow's extraordinary teaching ability showed itself early -- well before he became known for his research. Born in 1916 in a suburb of Philadelphia, he grew up in Wichita where he attended Friends University. His father was a professor there, and Jim took most of his biology courses from him. By 1936 Crow was involved with a pacifist group called the Emergency Peace Campaign where he discovered his knack for public speaking. He spent the summer traveling around western Kansas giving speeches for the group, and later said he has "never been afraid of an audience since that time." [1]

This ability served him well when he landed his first professional job at Dartmouth College. On short notice he was required to teach a wide variety of courses including genetics, zoology, embryology, parasitology, comparative anatomy, various math and statistics courses, and even navigation. This was during World War II, and some of the courses were aimed at preparing naval officers. Crow had to take courses in spherical geometry in order to teach navigation, and spend a month in Guatemala for training in parasitology. (When he arrived at the hospital in Guatemala, they told him every patient has three diseases: malaria, hookworm, and whatever he came to the hospital for. [1])

Crow perfected his teaching technique when he came to the University of Wisconsin in Madison where he spent the next 64 years. He taught a variety of genetics courses, especially general genetics and population genetics. His door was always open to students who wanted to talk with him. He always tried to learn the names of his students, and for large classes this entailed taking a photo of each student on the first day of each semester. He allowed that he wasn't the best photographer in the world, but thought he might be the fastest.

His lecture notes for general genetics were published under the title of "Genetics Notes" but were fondly known as "Crow's Notes" by generations of genetics students [2]. Crow's Notes eventually went through eight editions and was translated into many languages, including Korean, Dutch, Japanese, Portuguese and Serbo-Croatian. The early editions were published with every other page left blank so students could write their own notes. This useful feature had to be abandoned in later editions as the explosion in genetic knowledge would have made the volume too bulky. The examples and diagrams from Crow's Notes have become so ubiquitous in the teaching of genetics that many of us use them automatically without being conscious of their source.
An author of more than 250 papers on a wide range of genetical topics, Crow is especially known for his work in theoretical population genetics. His classic textbook, *An Introduction to Population Genetics Theory* [3], written with his former student Motoo Kimura, defined the field during the critical decades between the foundation of population genetics in the early 1900s and the modern era. Crow helped develop the infinite-alleles neutral model in which a mutation rate, $\mu$, in a population of effective size $N$ results in an equilibrium in which a fraction $1/(4N\mu + 1)$ of the individuals is homozygous. He refined the concept of genetic load to measure how the average fitness of a population can decline owing to factors such as mutation and selection in favor of heterozygotes. Crow's theoretical work also added depth to our understanding of areas as diverse as the role of sexual reproduction in evolution, the effects of meiotic drive, the genetic consequences of inbreeding, the detection of inbreeding in humans by name identity and the stochastic theory of genetics in finite populations. Crow's contributions to evolutionary theory were recognized in 2009 by the establishment of the J. F. Crow Institute for the Study of Evolution (http://www.evolution.wisc.edu).

Crow's experimental contributions began with his Ph.D. work on Drosophila at the University of Texas at Austin and continued at the University of Wisconsin. He was particularly interested in the accumulated effects of minor deleterious mutations. His work on Drosophila revealed much about the frequency of such mutations, their range of effects and their degree of dominance and epistasis. He thought that a model of approximate truncation selection may provide a way for populations to survive the onslaught of deleterious mutations. Crow's work in this area and his insights contributed much to the current view of how mutation rates affect human genetic health.

Perhaps as important as Crow's own research is the inspiration he gave to his students and colleagues. He often declined authorship of work done under his supervision. Kimura, while a graduate student of Crow, worked out the mathematical details of the fixation probability of neutral alleles, their time to fixation and their frequency distributions. This work later formed the foundation of what would eventually become Kimura's neutral theory which is now widely used in the interpretation of molecular genetic data. The discovery of Segregation Distorter in Drosophila and much of the early work on P transposable elements was also performed under Crow's supervision.

Crow's enthusiasm for science was beyond contagious; it was downright beguiling. In the late 1980s some local students and faculty had an informal evening discussion group about evolution. When it was Crow's turn to lead the discussion, the topic he selected was phase 3 of Sewall Wright's shifting balance theory. If anyone had asked me to choose an especially uninteresting topic, this selection would have been high on the list. At the time, Wright's shifting balance theory was already very much out of favor.
among evolutionary theorists. Its mathematical basis was vague and suspect, and the theory was increasingly considered unnecessary to explain the evolution of epistatic gene combinations, which was Wright's primary motivation for proposing the model. Moreover, of all the aspects of the shifting balance theory, phase 3 seemed to be the least interesting. According to the theory, the most critical event occurs in phase 2 when an epistatic combination of genes coalesces and becomes common within a subpopulation. After that, it is only necessary for migration to push this combination into other subpopulations. Therefore, had anyone else proposed talking about phase 3 of Wright's shifting balance theory, I would have been sorely tempted to skip that evening session. I did attend, however, and Crow worked his usual magic. By the end of the talk, I was so enthralled about phase 3 of the shifting balance theory that I wanted to work on little else for the next several months. Carter Denniston, another population geneticist in our department, was bitten by the same bug, and we commandeered every available computer to crank out calculations during the off hours. John Sved, who was on sabbatical in my lab at the time, caught the infection as well and helped with some of the theory as did Alexey Kondrashov. The work was eventually published in *Evolution* [4] and stimulated further research, including some in areas only remotely related to the shifting balance theory.

The list of Crow's graduate students and postdocs is long and star-studded. It includes a dynasty of outstanding Japanese students beginning with Kimura. Each member of the dynasty recruited his successor. Crow was widely known for his ability to get along with graduate students whose personalities or beliefs might make them difficult to deal with. Crow, whose self-deprecating description of his own political views placed him among the "confused liberals, slightly left of center, and do-gooders" [1], was able to work with students whose extreme left- or right-wing politics might have put them at odds with most mentors. Crow provided a solid anchor in scientific objectivity which was especially valuable for those students who felt themselves most strongly pulled by the currents of their own political views. In at least one case, a particularly brilliant but obstreperous student was specifically steered toward Crow's guidance because it was thought that no one else would be able to handle him.

Crow's reputation for rising above acrimony was well-earned, but it also earned him some difficult assignments. In 1998 the National Institute of Justice needed someone to head up a committee to study the use of DNA in forensics. This working group had the daunting task of merging the views of a diverse group of strongly opinionated experts in both legal and scientific fields. The choice of Crow for the job was inspired. The group's report, published in 2000, is highly regarded for its clarity and effectiveness. It serves as a model for the application of sound statistical methodology in evaluating evidence in legal settings.
Crow's easy humor and stabilizing presence could defuse even the most delicate situations. When I was a student in his lab in the 1970s, we had a visiting researcher who had spent most of her career in the Soviet Union. She was one of the few geneticists there who was able to continue working during the Lysenko era from the 1930s into the 1960s when many geneticists were punished, even executed, for practicing what was considered to be bourgeois pseudoscience. When she came to the United States in need of a lab, Crow offered her a technical position. She worked with Drosophila, and Crow gave her a laboratory room with bench space, a microscope and other supplies. However, being a few years older than Crow, she considered herself to be in charge of the entire laboratory and was soon disrupting our work by reassigning equipment and commandeering additional supplies. We had to ask Crow to intervene, even though we feared the situation would not end well for Crow's strong-willed guest. After all, someone who had stood up to the likes of Joseph Stalin and Trofin Lysenko was not likely to back down to a soft-spoken gentleman like Crow. We needn't have worried. The next morning all the equipment was back where it belonged, and there was no sign of any hard feelings.

The only time Crow's steady diplomacy seemed insufficient was when he was asked to comment on a 1969 article by Arthur Jensen on the race and IQ controversy. Jensen had been heavily criticized for his view that much of the variability in IQ was genetic. Crow wrote that he did not agree with many of Jensen's conclusions, but thought that Jensen was intellectually honest and that his quantitative methodology was sound. In those days, there was a common misconception that any nonzero heritability of IQ implied that racial differences were heritable. Crow understood that this was not the case and tried to explain it in a way that would be transparent to nonscientists. It wasn't enough. In the highly charged climate of the day, Crow found his classroom picketed, and placards abusing his name "Jim Crow" were posted outside the lecture hall. Crow must have known the effect his words would have, but he expressed his views with courage and honesty. Outwardly, at least, he handled the student protests with his usual good-humored aplomb until it blew over after a few weeks. If there was a silver lining to this episode, it was that all of us who knew Crow were left with a deeper understanding of the meaning of intellectual integrity.

Throughout his long career, Crow was sought after for administrative and public service tasks. He usually accepted. In addition to his central role in the DNA forensics commission, he was one of the key players in a series of National Academy efforts to define the effects of radiation on human health. He worked on these committees, often as chair, from the 1950s through the 1980s. This work resulted in the concepts of "doubling dose" and "mutational component" now commonly used in the field [5]. He has been president of the Genetics Society of America and of the American Society of Human Genetics. He has chaired various National Institutes of Health and National
Crow was nominally retired in 1986, but his work continued unabated until his death in 2012 just shy of his 96th birthday. One of the most appreciated tasks he performed in his later years was to co-edit the monthly "Perspectives" column in the journal Genetics. For more than twenty years Crow and his colleague William Dove produced these widely-read pieces on the history of genetics. Crow himself wrote 45 of the 296 articles to appear during this period -- by far the most of any author. Some of these, such as the opening article on Sewall Wright, Crow wrote because the topic was of special interest to him. Others, however, he wrote out of necessity because the designated author could not make the deadline. When that happened, Crow would simply take a couple of days off from his other tasks and write up an always-excellent piece for the column.

Although James Crow has received nearly every honor and award possible in his scientific field, there are many people who knew him primarily as a musician. He was an accomplished violist. He played in the Madison Symphony Orchestra for 45 years and served as president of that organization and of the Madison Civic Music Organization.

Crow's music forms a separate line from his scientific life and his family life, but the lines are not parallel. They intersect at some critical points. Crow met his wife, Ann, when they both played in a college orchestra. She played the clarinet and was seated fortuitously close to the string section. They were married for 60 years until Ann's death in 2001. They are survived by three children, six grandchildren and two great-grandchildren.

Crow also met his longtime friend and colleague, Carter Denniston, through music. Denniston was a graduate student in anthropology and played the cello. Crow convinced him to switch to genetics where he eventually received his Ph.D. and landed on the faculty in Crow's department in Madison. The two of them were collaborators in teaching and research for more than 35 years.

Crow was certainly a man of rare intellectual gifts. Rarer still is the combination of that intellect with enough energy and longevity to use it to its fullest. However, I think what made James F. Crow truly unique was a kind of balance he always seemed to possess. It made his towering accomplishments appear almost effortless. Like a tripod which owes its stability to the simple principle of three equally strong legs, Crow had his
science, his family and his music. The rest of us have his remarkable legacy of a deeper understanding.


Acknowledgements: The photo was taken by Millard Susman in 2005. Millard also contributed ideas and comments for this article.