IN MEMORIAM: WILLIAM T. KEETON

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William Tinsley Keeton, Professor of Biology at Cornell University, internationally known authority on bird orientation and navigation, and author of one of the most widely used biology textbooks, died of heart failure on 17 August 1980. He was 47 years old.

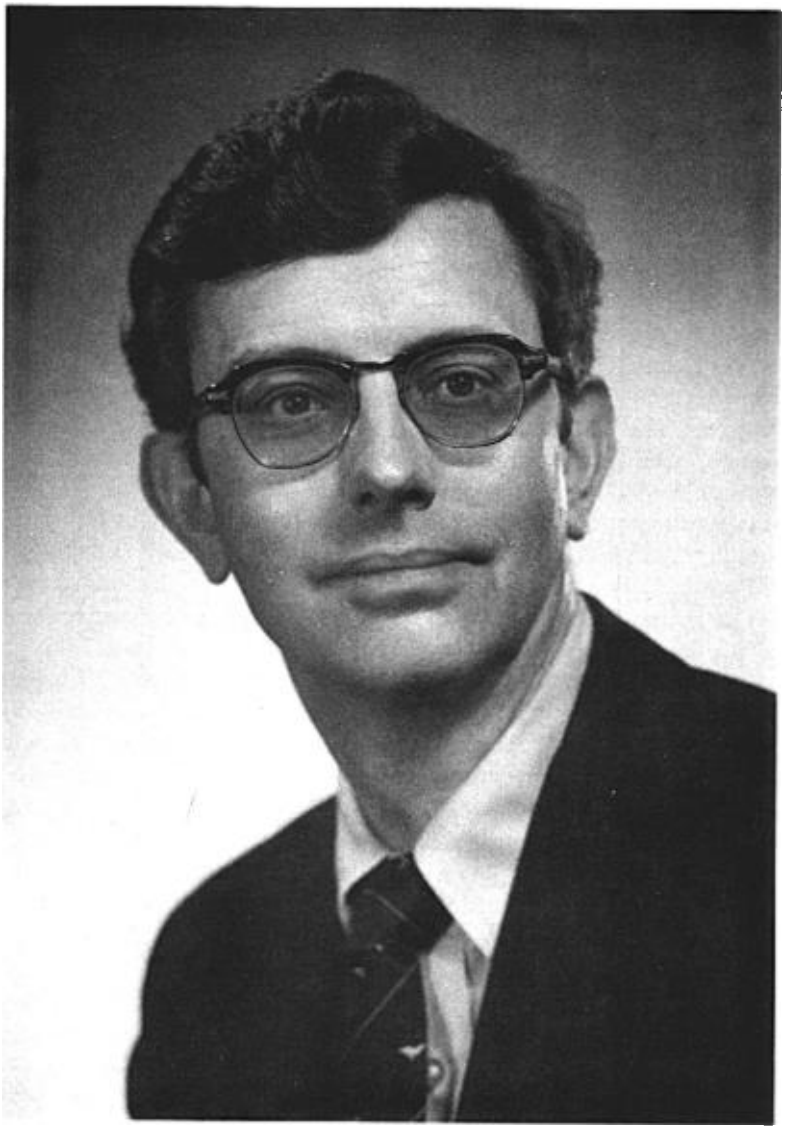
Bill Keeton was born on 3 February 1933, the son of William Ivie Keeton and Doris Tinsley Keeton. He grew up in Lynchburg, Virginia, and soon grew to love its rolling hills and forests. As a boy, he prowled those forests, bringing home assorted insects and reptilian pets. When only 9 years old, he obtained his first homing pigeons. The following year he and some friends built a loft, and from then on Bill's hobby was keeping and racing homing pigeons. Tending the pigeons was a family affair, and both parents helped to take the birds out for training flights. Bill's father worked as an engineer for the telephone company, a job that involved considerable travelling throughout the state. He routinely took Bill's pigeons along with him and then released them for distance training. But Bill's birds rarely were winners. The reason, he always claimed, was that his yard was surrounded by tall trees. After a race, his birds would return home quickly, but then land in the trees rather than entering the home loft. Since it is the elapsed time from release until entry into the loft that decides races, Bill seldom won. His father recalls how Bill would come home after school and, foregoing his homework, spend hours flying his birds. Bill was a careful observer of behavior even in those early days, and came to know his birds individually on the basis of their personalities.

During his high school summers, Keeton attended the Virginia Federation of Garden Clubs Nature Camp in the Shenandoah Valley of the Blue Ridge Mountains. His experiences here introduced him to the excitement that scientific investigation can bring to natural history. He never forgot this lesson, and he returned to this camp as counselor, director of instruction, and consultant later in his life.

After graduating from high school, he attended the University of Chicago, obtaining both the Bachelor of Arts and the Bachelor of Science degrees. He then returned to Virginia to pursue graduate work in entomology at Virginia Polytechnic Institute, where he received his master's degree. Here he met Barbara Orcutt, whom he married in the summer of 1958.

Keeton first came to Cornell in the fall of 1956 to conduct research on millipede systematics for his doctorate. In 1958, upon completion of his degree, he joined the Cornell faculty of Entomology.

One year later, he began teaching Cornell's introductory biology course, which soon became known on campus as the "Keeton course" because of his superior teaching style. He sought to combine botany and zoology into an integrated field, tied together by the unifying evolutionary threads of adaptation and natural selection. His creative approach to biology teaching won critical acclaim. The graduating seniors of 1966 awarded Keeton the coveted "Professor of Merit" award for outstanding excellence in teaching. Driven by his own enthusiasm for the course, and encouraged by the students' responses to it, he wrote his textbook, *Biological Science*, which first was published (by Norton) in 1967. He successfully translated his teaching skills into print. This was no small feat—it consumed his energies for most of 5 years.



WILLIAM T. KEETON, 1933–1980

But the result was awesome. His text, now in its third edition, has introduced hundreds of thousands of students to biology, and stimulated untold numbers to take up the field as a profession.

In his early years at Cornell, Keeton established himself as a leading scholar in the study of millipede systematics. He published numerous papers on the topic, and built up an important collection of study specimens. But his love for natural history continued. And so did his curiosity about pigeon homing.

He read the literature on orientation behavior and became convinced that there was much more to be learned. I remember that when I first joined the faculty at Cornell, I would tease Bill, asking him facetiously: "What makes you think that a millipede taxonomist can solve the mysteries of bird orientation?" And he would get

a twinkle in his eye and respond: "When I flew pigeons as a boy, they performed better than most of the results published in the homing journals. And furthermore, they homed under conditions when they shouldn't have been able to according to the literature." He was correct. By knowing the subtle nuances of pigeon behavior, and by spending time with his birds observing them as individuals, Bill (and most serious pigeon racers) had achieved homing results superior to those reported by scientists.

Keeton received his chance to enter the research arena of avian orientation in 1965, when Cornell reorganized its Division of Biological Sciences. Keeton played a major role in this reorganization, and moved from the Entomology Department into the newly created Section of Neurobiology and Behavior. When he did so, he began his vigorous research program into pigeon homing. Cornell built him a research loft, he obtained a small stock of breeding birds, and field studies were under way.

He soon discovered that pigeons, if allowed to train under overcast skies (which abound in Ithaca, New York), could home perfectly well without having to observe the sun. Thus, even though the sun remained a dominant cue when it was visible, pigeons could use a "back-up" homing mechanism in its absence. The search for the elusive "back-up" led to another major finding: the ability of the birds to select a homeward direction under overcast skies broke down if small bar magnets were attached to their bodies. Keeton and others then began a series of studies to elucidate the role of magnetism in orientation. Interestingly, it was only the initial departure bearings, and not so much homing ability per se, that was affected by wearing magnets. Thus the pigeons behaved as though they could adjust their homing systems to still another, unknown, "back-up" in the absence of both celestial and magnetic information.

Such findings led toward a new philosophy of orientation research. Prior to such discoveries, workers had been seeking a unifying, single-cue theory to explain homing behavior. Keeton emphasized that birds can use multiple sources of information; that there is great redundancy in animal orientation systems. Redundancy, however, poses major problems for behavioral scientists. It means that unambiguous interpretations of experiments are not possible unless alternate cue systems are controlled simultaneously. And that is a tall, if not impossible, order. But the acceptance of redundancy also leads to a reexamination of previous data and theory. Differing hypotheses about cues used in orientation came to be viewed not so much as conflicting, contradictory models—but more as mutually complimentary pieces in the same master jigsaw puzzle of navigation behavior. Attention began shifting away from arguments over the merits of one cue system versus another, and toward questions such as: Is there a hierarchical nature to the different components of orientation behavior? If so, does it change with the age and experience of the bird? Does it also change with changing meteorological conditions? Or at different geographic locations? How do different cue systems come to be calibrated one against the others? And how do the different components of orientation behavior develop during the individual ontogeny of a given bird? Such questions were the foci of Keeton's attention in recent years, and will dominate work in the field of orientation for much of the next decade.

But it was more than the contents of his papers that made Keeton a great scientist. It was his enthusiasm for science and his dedication to excellence in all that he did.

He was completely open with his ideas and, if results happened to conflict with those reported from another laboratory, he would invite the principals to come to Ithaca to resolve the issues through collaboration. Each summer the Cornell Pigeon Loft became a focus of frenzied activity. Two thousand pigeons were kept here, and numerous students and technicians continuously were busy training and conducting experiments with them. The loft was an intellectual center, not only for these students, but also for visiting colleagues and collaborators from around the world.

Keeton was often honored for his contributions. He held a Liberty Hyde Bailey chair professorship, and recently had been elected to serve on Cornell's Board of Trustees. He had been a visiting professor both at the Max-Planck-Institut für Verhaltensphysiologie (Seewiesen) and at the University of Konstanz, in Germany. He had been awarded the honorary Doctor of Science degree from Coe College in Iowa. In 1978, he had been an invited plenary speaker at the XVII International Ornithological Congress in Berlin. He delivered the keynote address at the College Station, Texas meeting of the A.O.U. in 1979. And, just this past August, at its annual meeting in Fort Collins, Colorado, the A.O.U. elected him a Fellow.

Science, in a way, is like a game. The scientist plays the role of detective in trying to solve a difficult mystery. In orientation work, experiments are the medium through which we "interrogate" our subjects, trying to force them to reveal clues. Many clues are false, and only replication and new experimentation finally separate the true from the false. Each clue points the way toward another, in a never-ending chase for knowledge. To a scientist, nothing is more intellectually stimulating than being on this chase. William Keeton knew the game, and played it exceedingly well. He also loved it, and his enthusiasm was contagious to all of us fortunate enough to have worked closely with him.

Eventually, enough clues will be available to begin piecing them together into a coherent "solution" to the mystery. We in orientation research have not yet found that solution, but we feel that we are getting close. And this, in no small measure, is due to the far-reaching contributions of William T. Keeton.

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