Obituary

Thomas A. McMahon (1943–99)

Biomechanist who discovered fundamental principles of biological structure and function

Thomas A. McMahon, who died suddenly on 14 February, was a pioneer in the field of biomechanics, a discipline that integrates engineering and biology. During his 30-year career at Harvard University, McMahon sought the fundamental mechanical principles that determine how organisms are built and work. Today, most biomechanists specialize in one or maybe two sub-disciplines, such as the mechanics of fluids, plants, bones, muscles or locomotion. McMahon contributed to each of these areas — not as a dabbler, but as a penetrating thinker who identified the key mechanical parameters that shape biological structure and function.

McMahon liked to integrate his hobbies and science. He enjoyed rowing his single shell on rivers and lakes. After observing that larger shells with more rowers could glide past him at high speed, he developed a simple mechanical model to explain why. McMahon's rowing project catapulted him into the world of biological scaling, a transition that led him to develop the theory of 'elastic similarity'. The guiding principle of this theory is that organisms of different sizes are built so that their structures experience similar elastic deformations in their everyday lives. McMahon measured the dimensions of animal bones and trees to see how plausible his theory was. He spent a sabbatical in Vermont, dismantling and measuring the dimensions of an entire tree, and discovered that longer tree limbs are relatively stouter than shorter limbs. As a result, all limbs droop to a similar angle under their own weight — as predicted by the elastic similarity theory.

In 1969, McMahon met the late C. Richard Taylor, a fellow Harvard professor and comparative physiologist, who profoundly influenced McMahon's career by introducing him to the mysteries of animal locomotion. McMahon's interactions with Taylor were extraordinarily fruitful because their scientific styles differed dramatically. When faced with a difficult question about how animals work, McMahon pulled out a piece of paper and derived a mathematical model to answer the question. In contrast, Taylor designed an elegant experiment. Although McMahon and Taylor did not publish many papers together, they shaped the scientific styles of their students, many of whom learned the power of bringing together models and experimentation. McMahon's view of how mathematical modelling can be used to understand locomotion is demonstrated in his influential book *Muscles, Reflexes and Locomotion* (Princeton Univ. Press, 1984).

After turning his attention to locomotion, McMahon revolutionized our understanding of walking and running by emphasizing how the mechanical properties of the body influence locomotor movements. McMahon and Simon Mochan developed a 'ballistic walking' model, which demonstrated that the swing limb of a walking human behaves like a passive compound pendulum, and that it is coupled to the stance limb, which behaves like an inverted pendulum. They concluded that the coupling of these pendula is critical in determining the walking motion. The plausibility of this idea was later proven when Tad McGeer invented a passive robot that walked by using these pendular mechanisms.

McMahon continued to show that the body's mechanical properties are crucial for shaping locomotion, when he worked out how the spring-like stiffness of the legs determines running dynamics. This discovery led to the invention of the 'tuned track'. McMahon and Peter R. Greene realized that, by matching the stiffness of the track to that of the human leg, they could increase running speed. Indeed, after their tuned track was installed at Harvard, performances in the quarter mile and longer races improved by about 3%. Later, work by McMahon and others revealed that this spring-like behaviour of limbs might be an organizing principle of the neuromuscular system when animals run, hop or trot.

Locomotion biomechanics and fluid mechanics are usually separate sub-disciplines of biomechanics, but McMahon and James W. Glasheen combined them to explain how basilisk lizards — also called 'Jesus Christ' lizards — can run on the surface of water. These lizards use three tricks to do this. First, the lizard's fringe-toed foot slaps the water surface, and then it rapidly strokes downward creating an air cavity. Both the slap and stroke contribute upward impulse, preventing the lizard from sinking. Finally, the lizard pulls its foot upward before the air cavity collapses, so minimizing the downward drag force on the foot.

McMahon enjoyed inventing practical devices that were inspired by his biomechanical knowledge. Recently, with Wilson C. Hayes and Stephen N. Robinovitch, he designed an ingenious device to reduce the risk of hip fractures when elderly people fall. They invented a U-shaped hip pad that surrounds the head of the femur. Composed of a material that is normally liquid, this pad conforms to the body during the slow movements that occur during everyday activities. But during the impact of a fall, rapid deformation of the material stiffens it into a solid, which shunts force away from the head of the femur and into the surrounding muscles and fat.

McMahon told his friends that he had "the best job in the world", because his duties included discovering how nature works and interacting with bright young students. His reputation as a thoughtful and caring mentor led Harvard to install a bench outside his office door to accommodate the perpetual queue of students seeking guidance. McMahon was modest, unconventional and playful. His golden retriever, Tess, accompanied him everywhere, even to traditional social affairs on the Harvard campus. He often invited students to join him for "fetch breaks" — respites from academic work, to play with his canine companion on the lawn outside his office. McMahon was also an acclaimed novelist. He wrote three novels, all of which featured scientists, engineers or inventors as the main characters.

McMahon wrote about his view of the interplay between scientific progress and nature's mysteries: "Theories rarely threaten the mystery of natural phenomena. The best theories harmonize with that mystery and make it ever more fascinating". Indeed, McMahon's melding of engineering and biology to discover how organisms work did just that.

Claire T. Farley

Claire T. Farley is in the Department of Integrative Biology, University of California, 3060 Valley Life Sciences Building, Berkeley, California 94720-3140, USA.

e-mail: cfarley@socrates.berkeley.edu