R. McNeill Alexander

(1934–2016)

Zoologist who pioneered comparative animal biomechanics.

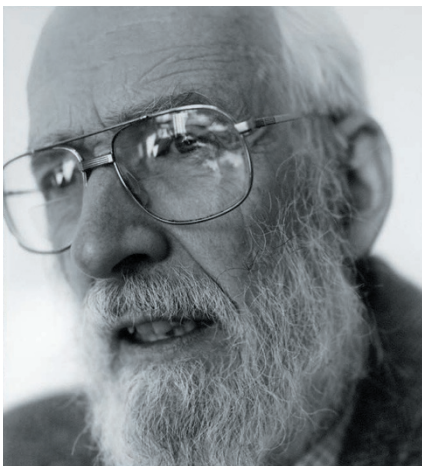
Robert McNeill Alexander defined many fundamental properties of how animals move. He combined elegant mechanical and mathematical analyses to reduce problems in flight, swimming, walking, running and anatomy to their simplest level. He explained the importance of inertial forces versus gravitational ones in determining which gaits land animals use to move at different speeds, and he predicted the pace at which dinosaurs probably moved.

His work showed why animals of different sizes move in similar ways, as well as the importance of the elastic energy stored in tendons in reducing the metabolic cost of jumping and running. Alexander wrote 20 books, including his classic text *Animal Mechanics* (Sidgwick and Jackson, 1968). He published more than 280 scientific papers. On most subjects in biomechanics, it would be wise to first read what Alexander had to say.

Born in 1934 in Lisburn, UK, to the chief engineer of the city of Belfast Robert Alexander and author Janet McNeill, he was inspired at school by his biology teacher Arnold Benington, a BBC radio naturalist. Aged 16 or 17, Alexander published his first paper 'Behaviour of the robin during laying' (*Brit. Birds* **44,** 389–390; 1951), after a pair nested on top of a wardrobe in his bedroom. That year, he also won an essay prize from the Royal Society for the Protection of Birds for an experiment to test if birds would remember which trough on his windowsill contained hidden food.

At the University of Cambridge, Alexander read natural sciences. He completed a PhD on the function of swim bladders in fish. His supervisor was James Gray, a pioneer of comparative experimental studies of animal locomotion. He also acted, including a memorable appearance as the giant Harapha in a production of John Milton's *Samson Agonistes*. And he travelled extensively in Europe, meeting his wife Ann, also a student at Cambridge, on a trip to Italy in 1956. He was an expedition scientist on a Cambridge trip to the jungles of Guyana in 1960. After a lectureship at the University College of North Wales (now Bangor University) from 1958 to 1969, Alexander became professor of zoology at the University of Leeds, until his retirement in 1999.

In the early 1960s, the functional analysis of animal form was driven by descriptive comparisons of morphology that largely lacked mathematical expression. Alexander addressed this by combining field studies with laboratory experimentation and



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theoretical modelling. In collaboration with Harvard University physiologist C. Richard Taylor and Kenyan veterinary scientist Geoffrey Maloiy, he examined movement in African mammals as diverse as dik-dik and buffalo. He formulated a model that explained how and why animals move in similar ways, and he used Froude numbers (previously deployed by Victorian engineer William Froude in his analysis of the bow waves of ships) to explain how the length of limbs affects speed and gait over ground. Alexander also built theoretical models of foraging and migration, suggesting that only birds or large mammals benefit from the risks and energy costs of long-distance travel.

Alexander compared the athletic performance of humans with that of other animals. He discovered that small animals rely on the rapid release of elastic energy stored in their tendons to jump high and far, whereas humans and larger animals stretch their muscles with force to achieve greater heights. And he evaluated the evolutionary and energetic consequences of building and maintaining physiological and mechanical structures that are necessary for locomotion, such as those that facilitate respiratory gas transport and musculoskeletal support.

His family indulged his research endeavours. In the 1970s, while developing an approach to derive the speeds of dinosaurs from their fossilized tracks, Alexander took his two children to Snettisham beach in Norfolk, UK. There, they walked and ran along various textures of mud, counting their strides and timing themselves with a stopwatch. These antics are recorded in the paper 'Estimates of speeds of dinosaurs' (*Nature* **261,** 129–130; 1976).

Alexander's work fuelled the emerging field of biorobotics. He participated in a European effort to build a robot dinosaur, advising on the probable gait and a simplified arrangement of joints for the creature. His findings also contributed to improved gait rehabilitation and prosthetic devices for people. His coffee-table book *Bones* (Prentice Hall, 1994) reveals the beauty inherent in the biomechanics of animals. His 1995 educational CD *How Animals Move* was widely used in schools and universities; it remains the best teaching aid of its kind.

Neill was devoted to comparative biomechanics and its wider appreciation. He served as secretary to the Zoological Society of London from 1992 to 1999 (after the reversed decision to close London Zoo). He served as president of the Society for Experimental Biology and the International Society of Vertebrate Morphology and as editor of the journal *Proceedings of the Royal Society B*. Among his many honours, Neill was elected fellow of the Royal Society in 1987 and appointed Commander of the Order of the British Empire in 2000. The gong that gave him the most amusement — and best captured his Gandalf-like status — came in 1996, when British newspaper *The Mail on Sunday* listed him as one of "Britain's Nuttiest Professors — Ten Sages Who Really Know Their Onions".

In retirement, Neill continued to attend professional meetings, give lectures and serve on examination committees. He advised on television documentaries, including the BBC's 2001 series *Walking with Beasts*. As a reviewer, he was always succinct, insightful and supportive of good science. He visited every poster at conferences, where he conveyed his passion to students and remained a role model. Neill was warm and animated in conversation and broad-minded when communicating his science. He was an inspiration and generous mentor to many of today's leaders in the scientific field that he established. ■

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