

OBITUARY

Professor Robert McNeill Alexander CBE FRS (1934–2016)

Robert F. Ker*

Robert McNeill Alexander, known to friends and colleagues as 'Neill', was a zoologist with an engineer's eye for how animals work. He used mathematical models to show how evolution has produced optimal designs. His skill was to choose appropriate models: realistic enough to contain the essence of a problem and yet simple enough to be tractable. He wrote fluently and easily: 23 books, 280 papers and a CD-ROM entitled *How Animals Move*.

Neill was born in Northern Ireland on 7 July 1934. At his first school, in Lisburn, his closest friend was Michael Bennington, with whom he shared an enthusiasm for bird-watching. Michael's father, Arnold Bennington, taught biology at the school and was a BBC radio naturalist for Northern Ireland. Arnold included Neill in the Northern Ireland team for inter-regional nature quizzes on BBC Children's Hour.

Neill's parents decided to send him to secondary school in England. He gained a scholarship to Tonbridge School, where his uncle, James McNeill, was a housemaster.

In 1948, during the Easter holidays, a pair of robins built a nest in a cardboard box in his bedroom – the window was always sufficiently open. He sent his observations to David Lack, author of *Life of the Robin*, who encouraged him to submit them for publication in *British Birds*. The paper came out in 1951 while he was still at school.

Coming up to the University of Cambridge in 1952, Neill had expected to focus on chemistry. However, he was enthused by practical classes in zoology and, following a field trip to Flatford Mill at the end of the first year, he changed his emphasis to zoology.

After graduation, he continued in the Department of Zoology at Cambridge for a doctorate with George Hughes as his supervisor. He was to work on the supposed role of the swimbladder as a depth sensor. For 16 months he made no progress – he could not get the neurophysiology to work. Then, Ken Machin, a physicist who had been appointed to help zoologists with physical aspects of their work, suggested switching to the mechanics of the swimbladder. Neill did the research and wrote his doctoral thesis in 19 months. The swimbladder work led to four papers published in the *Journal of Experimental Biology*.

Neill was appointed to a lectureship in Bangor, North Wales, in 1958. For the first 2 years, he had little time for research because of the demands of lectures. He had to overcome a stammer and was tense before lecturing. However, his lectures were well received and he established an excellent rapport with the students.

In 1961, he married Ann Coulton, whom he first met when they were both at the University of Cambridge. Their daughter, Jane, was born in 1962 and their son, Gordon, in 1964.

University of Leeds, c/o 2 Hatton Place, Edinburgh EH9 1UD, UK.

*Author for correspondence (r.f.ker@leeds.ac.uk)

10 R.F.K., 0000-0002-6029-8609



Once the pattern of his teaching was established, Neill was able to devote a large proportion of his time to research. Among the topics he tackled was the mechanics of the protrusion of fish jaws during feeding, which, for best effect, must be done as fast as possible. This work was the start of his interest in the performance of the muscles of living animals during strenuous activities.

While at Bangor, as well as numerous papers, he wrote two books '*Functional Design in Fishes*' and '*Animal Mechanics*'. The latter is his best-known book (1st edition 1968; 2nd edition 1983). In these books, he developed the habit and skill of using simple calculations to confirm the plausibility of explanations. This skill became the hallmark of all of his scientific work.

In 1968, he was appointed to the Chair of Zoology at the University of Leeds. Neill and Ann found a house 2.3 miles from the university in a quiet location with a great view over a wooded valley. Neill's daily exercise was to walk to and from the university.

In his teaching, he instituted an undergraduate course on animal biomechanics, perhaps the first ever specifically devoted to this field. Instead of practicals, he suggested a list of small projects to be tackled by groups of two to four students. Each group did a different project. Many of the students developed a strong sense of commitment to their project and, over the years, several projects led to published papers. The system worked well until the 1990s, when the huge class sizes made it impractical.

On coming to Leeds, Neill changed the main focus of his research from fish to the locomotion of terrestrial vertebrates, which allowed him to more easily relate the physiological properties of muscles to their performance in intact animals. Anatomical measurements were made during dissection, ideally of

the animal that had been filmed earlier, though sometimes a similar animal was the best available.

In 1971, he published a small book entitled '*Size and Shape*'. This was his first excursion into scaling, which was to become a major theme in his research. In 1973, he was invited by Professor Knut Schmidt-Nielsen to join the planning committee for the Scaling Conference held in Cambridge (UK) in 1975. Neill's presentation to the conference related stride length, speed and gait for animals of a wide range of sizes.

He used this relationship to estimate the speed of dinosaurs from fossil footprints. The published data on locomotion were for hard ground rather than the soft ground the dinosaurs were on when they made the footprints. Therefore, Neill made his own measurements with his family as subjects running on a soft beach. As the children were then 13 and 11, this provided a variety of sizes of animal. The resulting paper was published in *Nature* (1976).

At the invitation of Professor Geoffrey Maloiy, he visited Kenya for fieldwork on four occasions, the first being in 1976, which resulted in nine papers over a period of 6 years: one paper for each week he was in Kenya. Some of the papers are on the mechanics of terrestrial locomotion and some on scaling.

By the late 1970s, he had estimates of the stresses on bones in many living animals. He compared these with the stresses at which the bones break. The ratio of these two stresses is the safety factor, a concept is familiar to engineers, but this was its first quantitative use in a biological context.

While working on locomotion, Neill became aware of the importance of spring elasticity in the muscle–tendon systems. He and Henry Bennet-Clark decided that the tendons, rather than the muscle tissue itself, were the main springs both for vertebrates and insects (Alexander and Bennet-Clark, 1977). When I came to work with Neill in 1978, my task was to investigate the mechanical properties of vertebrate tendons to establish that they were appropriate for this role. The answer was 'Yes', but that was not the end of it. A research student, Xiao-Tong Wang, first observed the surprisingly high susceptibility of tendon to fatigue damage and its systematic variation between tendons. This became an ongoing research topic and many questions remain unanswered.

As well as his research assistants and doctoral students, Neill worked with numerous colleagues both within Leeds and from other universities. These included Mike Bennett and Graham Askew (University of Leeds), Richard Taylor and Andy Biewener (Harvard University), Alberto Minetti (University of Milan), Adrià Casinos (University of Barcelona), Robin Crompton (University of Liverpool), Johan van Leeuwen (Wageningen University), Edwin DeMont (St Francis Xavier University), Richard Fariña (Universidad de la Republica, Montevideo), Larry Rome (University of Pennsylvania), Steve Wainwright and Steve Vogel (Duke University), Alan Wilson (Royal Veterinary College), Peter Aerts (University of Antwerp) and Dirk De Clercq (Ghent University). Teaching and research in biomechanics at Leeds were strengthened by the appointment of John Altringham as a lecturer in 1989.

Many contacts, and indeed friendships, started at conferences. Neill was a regular attendee at the Society for Experimental Biology annual conference, but, otherwise, all the meetings he went to were by invitation. The first invitation to a small, select symposium came from Knut Schmidt-Nielsen (Duke University). It was to the

Congress on Comparative Physiology held in Umbria, Italy, in 1972.

From the mid-1970s onwards, Neill set aside one lunchtime a week for an informal meeting of anyone interested in biomechanics. At various times, regular participants included members of the departments of Rheumatology, Physical Education, Anatomy and Applied Mathematics. These meetings were a key part of my decades at Leeds (1978 onwards).

Neill was a member of the Society for Experimental Biology from 1958 onwards, on its council from 1966 to 1968, vice president from 1993 to 1995 and president from 1995 to 1997. He was a Fellow of the Zoological Society of London from 1979 onwards, was elected to Council for a 3 year term in 1988 and served as Secretary from 1992 to 1999. His work helped to save London Zoo in a critical period. He was President of the International Society of Morphologists from 1997 to 2000.

Neill retired from his chair in 1999. Jeremy Rayner was appointed to replace him with the title of Alexander Professor of Zoology. As an Emeritus Professor, Neill still had an office in the university in which he worked, usually on three days a week.

Neill became editor of *Proceedings of the Royal Society B* in 1998. He retired from the editorship in 2004 and was replaced by Bill Hill, FRS, and a large team of associate editors.

In 2003 he became one of the ca. 100 members of the Board of Reviewing Editors for *Science*. He made preliminary decisions on about four manuscripts a week.

Following retirement, he wrote another major book, '*Principles of Animal Locomotion*', which is a lucid and authoritative account of locomotion on land, in water and in air. He was involved in three television series: *Walking with Beasts*, *The Future is Wild* and *Extraterrestrial*. *The Future is Wild* started by eliminating mankind, so that the remaining animals are then free to evolve naturally. For *Extraterrestrial*, Neill was required to dream up scientifically feasible lifeforms for strange planets. In both cases, he enjoyed having his imagination constrained only by the requirements of scientific feasibility.

He received many honours: CBE, FRS, EAS, FIBiol, MA and PhD Cambridge; DSc Wales; Hon DSc Aberdeen; Dr. h.c. Wageningen; and DSc Royal Veterinary College. He was awarded the Scientific Medal of the Zoological Society of London in 1969, the Linnean Medal for Zoology in 1979, the Muybridge Medal of the International Society for Biomechanics in 1991 and the Borelli award of the American Society of Biomechanics in 2003. He was elected a Fellow of the Royal Society in 1987 and was awarded a CBE 'for Services to Biology' in 2000.

He suffered from osteoporosis of the spine for the last 11 years of his life. His back became bent and he had increasing difficulty in walking. I last visited him on 4 March 2016, when we greatly enjoyed reminiscing about our many years working together. He died on 21 March 2016.

Acknowledgements

Neill wrote a draft of his own Biographical Memoir for the Royal Society in 2000, updated in 2005, and Gordon Alexander gave me a copy. I therefore acknowledge Neill's help in writing this obituary. Thank you Neill, yet again!

References

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