

OBITUARY

Colin James Pennycuick (1933–2019)

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Colin Pennycuick died on 9 December 2019 at the age of 86 years. He was a biologist who made ground breaking contributions to the understanding of animal flight performance, not only through his ingenious research (from novel electronics and instrumentation to glider and small aircraft field experiments) but also by popularizing the science and making his theory available to a wide spectrum of ornithologists and ecologists in the form of books, manuals and computer code. Colin was a keen birdwatcher from an early age, leading him to zoology studies at Merton College, Oxford, UK, followed by a PhD on muscle physiology at Cambridge, UK, in the early 1960s. His first scientific study on bird flight was on the gliding flight of fulmars, based on observations made during a trip to Spitsbergen, which resulted in his first paper in JEB (Pennycuick, 1960). The finding of his thesis work on frog fast muscle resulted in four companion papers also published in JEB (Pennycuick, 1964a, b, c, d). During university studies at Oxford and subsequent national service with RAF he trained as a pilot, which led to the common ground of the aerodynamics of aircraft and animals. After a postdoc studying the navigation of homing pigeons at Cambridge, Colin learned the tricks of training pigeons and set up a pigeon loft on the roof of the Zoology Department, Bristol University, UK, where he held a lectureship in 1964–1968. Here, he constructed and set up a wind tunnel in the stairwell of the zoology department and trained his pigeons to fly in it. At Bristol, Colin made a series of pioneering experiments of both gliding and flapping flight using the pigeons, which led to his adaptation of helicopter theory to bird flight, published in 1968 (Pennycuick, 1968a, b). The theory was refined over the next couple of years, and a complete version was published in a seminal 1975 chapter in *Avian Biology* (Pennycuick, 1975a). Another Pennycuick classic from this era is the 1969 Ibis paper ‘Mechanics of Bird Migration’, where the flight theory was used to derive migration performance and strategies in birds (Pennycuick, 1969).

In 1968, Colin took up a position in Nairobi, Kenya, and shipped the wind tunnel there, where it was used to study gliding flight in a fruit bat (after months of painstaking training to get the bat to let go of the perch). In Nairobi Colin obtained his own aircraft (a Piper Cruiser), which took him to the Serengeti research station in Tanzania where he was deputy director until 1972. Here, he took advantage of the natural bowl conditions and concentration of migrating mammals to make unique and penetrating observations on how they walk/trot/canter, how fast, and for what purpose (Pennycuick, 1975b). He also famously used a motor-glider to document the gliding/soaring flight of storks, eagles and vultures over the plains, again resulting in a series of classic papers which, amongst other things, compared their performance with his glider,



Colin making observations during field work in Iceland in 1995. Photo credit: Sverrir Thorstensen.

and with increasing detail with flight mechanics predictions (Pennycuick, 1971, 1972). When leaving the Serengeti, Colin took his aircraft, now modified for ‘long-distance flight’, and made a nine-stage return migration via Addis Ababa, Cairo and Crete, to Bristol where he remained resident until 1983. During this period he used the Piper to track migrating cranes in southern Sweden, and by using his own-designed ‘Ornithodolite’ – an instrument consisting of a range finder, wind anemometer and computer – he measured the flight speeds of mainly seabirds both in The Shetlands, UK, and Bird Island, South Georgia. In these studies he re-wrote the conventional explanations for why the albatross flies so elegantly and efficiently above a really turbulent sea (Pennycuick, 1982), and how and why different soaring birds have different planform shapes (Pennycuick, 1983). In 1983 Colin became the second holder of the endowed Maytag Chair of Ornithology in Miami, Coral Gables, USA, where he continued to make field measurements of bird flight performance using the Ornithodolite.

It was while in Miami that he developed his software ‘Flight’ and published the book ‘Bird Flight Performance: A Practical Calculation Manual’ originally accompanied by a floppy disk with the program (Pennycuick, 1989), and later made freely available online. During the Miami years, Colin obtained his own Cessna 182, and when leaving Miami in 1992, he made another inter-continental migration with his aircraft via Greenland and Iceland back to Europe.

It was at this time when A.H., as a graduate student, first met Colin when he came from Bristol to Lund, Sweden, in his Cessna for a project to track migrating swans passing southern Sweden. A.H. vividly remembers flying with him, assigned the task of ‘bird spotter’, how they circled at minimum turn angles (the stall warner disabled with duct tape) above flocks of migrating swans, and taking a GPS position each time passing right over the birds. On one occasion a flock of migrating Bewick’s swans were followed well off the southern Swedish coast and they inadvertently entered a

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military training area, which led to the Swedish air force sending a plane to inspect the strangely behaving Cessna.

It was also during these years that plans were hatched to construct a new wind tunnel specially designed for bird flight experiments, which specified that the entire tunnel should be tiltable to make gliding flight possible (as was the case with his original tunnels hung in stairwells in Bristol and between acacia trees in Nairobi). The tunnel was inaugurated in 1994 in the presence of the Swedish King, Carl XVI, who observed a thrush nightingale flying in the new wind tunnel. During the following years, Colin visited Lund regularly, usually staying in his Volkswagen bus conveniently parked in the carport of the wind tunnel building, and he installed various electronic gadgets he had designed for measuring flow speeds and flight performance of birds (Pennycuick et al., 1997). His vast experience and deep understanding of animal flight was decisive for the subsequent success of research at this facility. On one occasion, when we were plotting plans for measuring wake vortices by using a 'tuft-grid', Colin pulled up a small jar with downy feathers he had plucked from the heads of vulture chicks on a breeding cliff in the Rift Valley some 25+ years before as 'good to have stuff', suggesting we use them as airflow tracers. Even though this method never came to practical use, it illustrates how Colin saw opportunities in the most unexpected situations, such as climbing the nesting cliffs of vultures.

Between 2001 and 2015 Colin lectured on animal flight at the biannual graduate course on 'Ecology of Animal Migration' at Lund University, thus introducing generations of future researchers to flight biology and how to use his software for practical calculations of flight performance. Over his entire career Colin was faithful to his research on the biomechanics of animal flight. His empirical investigations on flight and migration performance were, with few exceptions, guided by his flight mechanical model that underwent several improvements based on new empirical data. His book 'Newton Rules Biology' took a more general view on questions about body size (Pennycuick, 1992), muscles as engines, fractal dimensions in biology and energy flow through ecosystems.

The impact of Colin Pennycuick's contributions to science surpass by far what most of us can hope for, and the 'Pennycuick model' of flight performance will be used by biologists and birdwatchers alike for many years to come. He received honours in the form of election to the Royal Society of London (FRS) in 1990 and an honorary doctorate at Lund University in 1996. Colin is survived by his wife Sandy, and his son Adam and his family.

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