CHARLES PORTER ELLINGTON

31 December 1952 — 30 July 2019
Charles Ellington graduated at Duke University, North Carolina, and came to Cambridge in 1973 to work for a PhD on insect flight dynamics. He developed novel methodology and software for the kinematic analysis of freely hovering insects and applied them to his own high-speed films of a range of species. He identified five new non-steady-state mechanisms for lift generation, was the first to develop a vortex theory for flapping flight and developed and extended the use of morphometric parameters in calculating the forces and power requirements of flight. He remained in Cambridge, married a colleague, joined the staff of the Department of Zoology, became a fellow of Downing College and continued to work on insect aerodynamics and energetics, publishing on flight muscle efficiency, the factors limiting flight performance and the aerodynamic implications of the origin of insect flight. Building a closed-circuit wind tunnel connected with a sensitive oxygen analyser, he studied with colleagues how the aerodynamics and metabolic power input of bumblebees vary with flight speed, challenging the orthodox theory that this should follow a U-shaped curve. Outstanding among later research was the discovery that hawkmoths, and by implication many other insects, gain high levels of lift by generating a vortex above the leading edge, stabilized by spiralling out along the span—a major focus of animal flight research ever since. His many administrative roles included editorship of the Journal of Experimental Biology. He became a British citizen in 1995, was elected FRS in 1998 and to a chair of animal mechanics in 1999. Awards include the Scientific Medal of the Zoological Society and the University of Cambridge Pilkington Prize for teaching excellence. He was diabetic throughout his adult life, and suffered progressive ill health following a heart attack in 1996. He took early retirement in 2010, lived quietly with his wife and two sons at home near Newmarket, and died in July 2019.
THE USA: CHILDHOOD, UPBRINGING AND EDUCATION

Charles Porter Ellington (known universally as Charlie) was born on 31 December 1952 in Prince George County, Maryland, USA, to Charles Porter and Margaret Mozelle Ellington, joining his four-year-old sister Martha. His father was then studying for a masters degree in agronomy at the University of Maryland, and continued to work for the university’s Extension service advising farmers on their crop production.

Charlie Ellington was a quiet, obviously gifted schoolboy with little interest in sports but excelling academically (figure 1). He had many friends, was involved in a range of academic clubs and activities and learned to play the clarinet in his free time. As he reached high school age he worked during the summers in commercial flower and tree nurseries, developing a particular interest in plants and the insects that visited them. Ominously, at age 17 he began to have health problems and was eventually diagnosed with Type 1 diabetes—a life sentence.

Graduating from high school in 1970 he moved with his parents to Athens, Georgia, when his father took a position at the University of Georgia. Charlie now entered Duke University, Durham, North Carolina. Owing to his exceptional academic record in high school and successful placement tests upon entering Duke, he was exempted from the courses needed to complete his Freshman year and so graduated summa cum laude in 1973—in three years, rather than the traditional four—gaining the Edward Horn Prize in Zoology and the Phi Beta Kappa award. Remarkably he was singled out at graduation by the president of the university as being the most gifted student ever to attend Duke.

Under the direction of Professors Stephen Wainwright and Stephen Vogel, Duke had become the fountainhead of biomechanics in the USA. Charlie Ellington was fascinated by this relatively new discipline, and, while still a student, collaborated with Vogel in research into the aerodynamics of ventilation of prairie dog burrows. Where next? Cambridge had been established as the centre of biomechanics in Britain by Sir James Gray FRS, Professor John Pringle FRS and others. Pringle had now moved to Oxford, and his place taken by Torkel Weis-Fogh, a brilliant, charismatic Dane who, like Pringle, had done pioneering work into the mechanics of insect flight. Charlie applied for, and was awarded, a Churchill Studentship to work for a PhD under Weis-Fogh’s supervision.

CAMBRIDGE, AND POSTGRADUATE RESEARCH

At that time the aerodynamics of flapping animal flight were still very poorly understood. Before the 1970s the principal approach had been the ‘quasi-steady’ assumption that the total aerodynamic force on the wings though a stroke cycle could be calculated by assuming that the forces on the wing at any instant were the same as they would be in a steady flow at the same velocity and angle of attack. The equations for this approach had been derived by M. F. M. Osborne (Osborne 1951) and used by Martin Jensen (Jensen 1956) in one of a series of classic experiments, jointly with Weis-Fogh, on the flight of desert locusts. These appeared to show that quasi-steady analysis was enough to explain forward flight in locusts, at least under the careful conditions of the experiment—the locusts were tethered in a wind tunnel, but supporting their own weight and controlling their own airspeed. By the 1970s, well aware of the limitations posed by tethering, Weis-Fogh with his photographic technician Gordon Runnells had moved into high-speed
cinematography of insects flying freely in laboratory enclosures, and he had now made a major breakthrough. Observing a range of species, he had calculated that, while the quasi-steady assumption appeared to be enough to explain hovering flight in bumblebees, chafer beetles, hawkmoths and drone-flies (Eristalis), all of which hovered with the body inclined and a nearly horizontal stroke plane (‘normal’ hovering), butterflies, other hoverflies and the tiny chalcid wasp Encarsia formosa required lift from previously unknown unsteady sources. He had proposed and named two novel mechanisms: ‘the fling’ in Encarsia and ‘the flip’ in hoverflies (Weis-Fogh 1973). These attracted wide interest beyond entomology, and a series of papers by fluid dynamicists followed (Lighthill 1973; Bennett 1977; Maxworthy 1979).

Charlie Ellington’s remit was to extend Weis-Fogh’s research to other insects, to seek other unsteady mechanisms for lift production, to develop methods to analyse flight sequences filmed at high speed and to quantify the forces involved. For a new zoology graduate, even one with the disciplinary breadth that a good American university provides, this presented huge practical and theoretical challenges. Tragically, in November 1975 Weis-Fogh took his own life, aged 53. By then it was already clear that Charlie would need appreciably more than the standard three years to complete his PhD research, and the loss of a supervisor at this stage could have been disastrous. The role was taken over by Kenneth Machin, a pioneering radioastronomer who had been persuaded by Pringle to join the Department of Zoology to provide expertise in physics and to collaborate with him in a now classic investigation into the mechanics of asynchronous insect flight muscle (Machin & Pringle 1959). Machin, a superb experimentalist, published little, but his technical flair was behind much of the excellent research in the department at that time. He proved to be the ideal replacement supervisor. Charlie shared both his general philosophy and his enthusiasm for designing and building
equipment—essential to this project—and their friendship and collaboration continued until Machin’s untimely death in 1988.

Charlie published three papers within the period of his PhD. The first was an able analysis of the fling mechanism—now referred to as the ‘clap and fling’—in *Encarsia* (1)*. The other two first presented (2) and then elaborated (3) a completely new vortex theory of flapping flight—the first such to appear in the literature. The crucial role of vorticity in lift generation had been recognized since the 1920s and the vortices developed by fixed aerofoils in steady flows were routinely studied in wind tunnels, but those generated in flapping flight, where wing velocity and attitude are constantly changing, were largely unknown and far harder to investigate. Charlie’s approach was to combine orthodox blade-element theory, as routinely used for fixed wing aircraft, with the momentum theory of helicopter aerodynamics, treating the area swept out by insect wings as a pulsed ‘actuator disc’, equivalent to the area swept by the helicopter rotor blades.

Cambridge recognized the importance of the ongoing research and allowed Charlie extra time to complete, employing him as a university demonstrator when the scholarship ended. This position was effectively a junior lectureship with teaching and research responsibilities, and Charlie’s appointment while still a PhD student reflected his evident outstanding potential. Downing College subsequently appointed him as a research fellow. His thesis, ‘The aerodynamics of hovering insect flight’, was eventually submitted in 1981, and the degree awarded in 1982. It was of astonishing quality, amply justifying the time taken for its completion, and was in due course published virtually intact as six seminal papers in a single issue of *Philosophical Transactions B* (4–9).

The importance of these papers cannot be overstressed; they provided the platform on which most subsequent research into insect flight mechanics has been built. Building his own digitizer and programming a vintage computer, the size of a wardrobe, Charlie had developed the first methodology for rigorous analysis of the kinematics of freely hovering insects. He had applied this to a range of species, distinguishing three types of hovering and discussing the probable airflow and vorticity involved in five new potential unsteady aerodynamic mechanisms for lift production. His novel vortex theory was now presented in full, and applied to estimate the circulation and associated lift production around flapping wings, exploring the combined roles of wing rotation and accelerations in generating the necessary transient elevated forces to support the body. He had developed an innovative morphometric approach to insect structure, emphasizing the importance of the moments of area and mass and of the ‘added mass’ of the air attached to the moving wings in estimating the aerodynamic and inertial energy demands of flight, incidentally finding that wing shape could usefully be described by a single parameter—the dimensionless first moment of area about the wing articulation. Morphometrics, kinematics and aerodynamics were then combined to derive equations for lift and power for both the quasi-steady mechanism of wing translation and the unsteady mechanisms of wing rotation. These were then applied to the insects analysed, and the results were combined with calculations of mean profile power and mean inertial power and of elastic energy storage in the muscles and cuticle to reach estimates of the total power requirements for hovering flight.

* Numbers in this form refer to the bibliography at the end of the text.
Marriage, Tenure and Flight Muscle Efficiency

Charlie was now firmly established at Cambridge, was elected a fellow of Downing College in 1979, and in 1984 was appointed as lecturer in the Department of Zoology.

In June 1977 he had married Stephanie Buckley, a reproductive physiologist then working on egg development in octopuses, and later on mammalian development. Stephanie, born in Teddington, was educated at City of London School for Girls and Sir John Cass College, London. She had moved to Cambridge after graduating, and worked as a technician with Martin Wells before converting to a PhD with the support of Wells and Weis-Fogh. She was by now an affiliated lecturer in the Department of Physiology and a fellow, lecturer in physiology and tutor at New Hall. It was the beginning of an exceptionally happy marriage (figure 2).

In the 1970s/80s, insect flight was a small field. Pringle, the acknowledged authority of the previous generation, had moved to the Linacre Chair at Oxford and thereafter contributed little more on flight. The only significant established insect flight group was that of Werner Nachtigall in Saarbrücken, which combined morphological and physiological research with aerodynamics, but they were filming only tethered insects. So was Andrei Brodsky, who was beginning investigations at Leningrad University; he and his co-workers were to make major contributions in the following years. I and my students were starting up at the University of Exeter, relating free-flight kinematics to the structure and deformations of the wings. But Charlie Ellington’s outstanding PhD research established him as the undisputed world leader in insect aerodynamics and flight energetics, and these two areas dominated his research for the rest of his career.

So far he had been concerned only with hovering flight—simplest to film and analyse as the insects remain in the camera’s field of view and flight velocity can be assumed to be zero. His calculations had cast doubt on Weis-Fogh’s conclusion that ‘normal’ hovering did not require unsteady lift. Was quasi-steady lift enough for forward flight—theoretically less expensive—or were unsteady mechanisms always needed? Was elastic energy storage and return between half strokes always necessary? How efficient was insect flight muscle?

Insect flight muscles are of two main types: close-packed synchronous muscle, which, like those elsewhere, need at least one nerve impulse for each contraction; and fibrillar asynchronous muscles, unique to insects, which are stimulated to shorten several times per impulse by being stretched by their antagonists while still contracting. While many insect orders have only synchronous muscle, Diptera, Hymenoptera, Coleoptera, Heteroptera and several groups of Homoptera all have asynchronous muscles powering the wing stroke. Where necessary, these allow far higher wing-beat frequencies than synchronous muscle permits and have allowed many insects to evolve to be tiny. Machin & Pringle (1959) had shown that asynchronous muscle can store energy elastically between contractions, and the cuticle, which in places includes the ultra-resilient elastomeric protein resilin, provides further scope for absorbing and restoring inertial energy between half strokes and significantly reducing the power output necessary for flight.

Charlie Ellington had provided values for the specific mechanical power output per kilogram of muscle mass required for hovering flight, comprising the aerodynamic power to move the wings through the air and the inertial power to accelerate and decelerate the wings and the added mass of air carried with them. The inertial power requirement depended on the amount of energy stored elastically: if this was high, the inertial requirement would be minimal; if low, the requirement would be high. Now (10) focusing on the bees Bombus and...
Figure 2. Charlie and Stephanie Ellington’s wedding, 18 June 1977. The best man was Steven Schwartz, later professor of space physics and director of the Space Laboratory at Imperial College. (Online version in colour.)

Apis and the hoverfly Eristalis, all of which have asynchronous muscle and for which data on metabolic power input were already available, he found that if elastic storage was assumed to be high, muscle efficiency must be between 5% and 8%, far lower than previous estimates had suggested. Conversely if storage was negligible, efficiency would fall somewhere between 12% and 29%. For comparison he reanalysed existing data for locusts and katydids, both of
which have synchronous muscle, and calculated that previous estimates of muscle specific power output and hence of muscle efficiency had again been too high. Overall he concluded that the maximum power output for all these insects would be enough for their aerodynamic needs, but not to overcome inertia; elastic energy storage would be necessary.

**FORWARD FLIGHT: AERODYNAMICS, POWER REQUIREMENTS AND THE POWER CURVE**

Charlie’s attention now turned to forward flight. How did body and wing kinematics alter with speed? What aerodynamic mechanisms were employed? How did power requirement vary with speed and how was it apportioned? New techniques were required. For rigorous kinematic analysis, the insect would need to remain in the high-speed camera’s field of view for several stroke cycles at a range of measured and preferably operator-controlled airspeeds. Metabolic power input could be calculated from rate of oxygen use—but how to measure this, when intake was through multiple spiracles?

These difficulties were approached in stages. Charles David, at Imperial College, had pioneered a method of optical tethering, whereby an insect could be ‘tricked’ by rotating optical stimuli into flying into a controlled airstream while remaining geostationary (David 1979). Supervised by Charlie, Robert Dudley, another Duke graduate who had similarly come to Cambridge on a Churchill Studentship, used an open wind tunnel flanked by rotating drums helically striped like barbers’ poles to ‘optically tether’ bumblebees in front of the camera at airspeeds from zero to 4.5 m s\(^{-1}\). The same analysis software developed for the hovering studies was used to measure stroke frequencies and amplitudes, wing tip paths, angles of attack and body angles, at a range of advance ratios—the ratios of forward speed to flapping speed—from 0 to 0.58 (12, 13). He found that neither frequency nor amplitude altered with speed, and concluded that this must be controlled by varying the angle of attack and the angles of the wing stroke plane and of the body to the horizontal. Measuring how lift and drag of detached wings varied with angle of attack and flow velocity in steady flow allowed the overall forces of the stroke cycle to be calculated using the quasi-steady analysis, and these were found to be inadequate for flight: unsteady lift would be needed at all the measured speeds (figure 3).

More surprisingly, power output was found to be independent of airspeed throughout the range. How could this be? The accepted view for animal flight, first proposed by Colin Pennycuick (FRS 1990) (Pennycuick 1968), and developed by Jeremy Rayner (Rayner 1979, 1988) was that a plot of mass-specific power requirements against speed should follow a U-shaped curve: highest in hovering, where the induced power—the component needed to generate lift—was maximal, falling to a minimum at intermediate speeds and rising again as the profile drag of the wings and the body drag increased with speed.

The next logical task was to measure how metabolic power input varied with speed. This was tackled in a series of elegant experiments in collaboration with Machin and Tim Casey of Rutgers University, New Jersey, in which bumblebees were flown, optically tethered, in a closed-circuit wind tunnel connected to a commercial oxygen analyser that had been modified by them to unprecedented sensitivity (14). Input, too, proved to be independent of flight speed in the range examined—up to 4 m s\(^{-1}\). Charlie concluded that the power curve of some flying animals was J-shaped rather than U-shaped, with power requirements similar for hovering
Figure 3. Wingtip path and body angles of the bumblebee *Bombus terrestris* at a range of airspeeds and advance ratios ($J$). Resultant aerodynamic forces are shown for representative downstrokes and upstrokes. (From (31), reproduced with permission from the *Journal of Experimental Biology*.)

and low and moderate speeds, rising only at high speeds. Heretically, in his next paper (15) he challenged the accepted view, again following Pennycuick (1968), that power imposes an intrinsic limit on animal flight performance, restricting large animals to an increasingly narrow speed range around the trough of the U-shaped curve. Instead, he suggested that limitations on low speed flight were aerodynamic rather than energetic, a result of an adverse scaling of lift production with body size: in isometric animals, lift coefficients should scale as $\text{mass}^{1/3}$.

Under his supervision, Alison Cooper explored these issues in bumblebees—ideal subjects as their wing loadings are exceptionally high for insects, and are increased still further by carrying loads when foraging. She found that the bees achieve higher lift coefficients when incrementally loaded by increasing their stroke frequency by up to 15%—within the limit imposed by the resonant properties of the system—and the amplitude by a similar percentage. Neatly, raising frequency would reduce the induced power requirement, offsetting the increase in profile power so that no extra overall power would be necessary in the low to moderate speed range, but the requirement would rise at higher speeds. For bumblebees, at least, the J-shaped curve was confirmed (Cooper 1993). For this work, she received special commendation in the Thomas Henry Huxley Award of the Zoological Society of London.

**Family, Administration and Teaching**

Charlie was now firmly settled in the UK, with no intention of returning to America. He and Stephanie moved from Cambridge to a thatched cottage in the village of Woodditton, near Newmarket. The family was growing: Matthew was born in 1988 and Nicholas in 1990. Ever practical, Charlie designed and built a garage with a loft for the boys to play in, and
developed the garden, with a pond to attract dragonflies and other wildlife. Frogs and toads soon moved in.

Stephanie was now working full-time in the Department of Physiology as a research assistant and as admissions tutor at New Hall. Charlie was taking on new responsibilities in the department, the college and beyond. He served on the SERC Post-Doctoral Fellowship Panel in 1985 and the SERC Animal Sciences and Psychology Sub-committee from 1986 to 1989. From 1990 to 1994 he was editor of the *Journal of Experimental Biology* (*JEB*), first alone, then jointly with the late Robert Boutilier. The *JEB* office was in the same corridor as the flight laboratories and was notable for its humour as well as its efficiency. Many contributors to the journal will remember—and probably still value—two Christmas cards from that time. The first, reproduced here (figure 4), showed the editorial team in ludicrous Christmas costumes. The second was a bogus, but convincing, cover of the journal, with a contents list of (just) plausible titles by familiar contributors, wrapped round a block of expanded polystyrene. It is said that several puzzled recipients missed the joke and wrote asking for the missing pages.

Charlie was proving to be an excellent teacher, with a special flair for making mathematical biology and advanced quantitative physiology both comprehensible and entertaining.

Figure 4. The *Journal of Experimental Biology* editorial team, Christmas 1992. Standing: left to right, Charlie Ellington, William Foster (assistant editor), Elizabeth Howes (assistant editor). Seated: Robert Boutilier. Kneeling, centre: Sandra Ray (editorial assistant). The reindeer was Jean Wallis, and the snowman Tom Matheson. (Used with kind permission from The Company of Biologists Ltd.) (Online version in colour.)
Particularly acclaimed was a first year course in quantitative biology that he developed, organized and taught for many years. Much later, in 2007, he was awarded the university’s Pilkington Prize for outstanding teaching for over 30 years (figure 5).

AERODYNAMICS RESUMED: THE ORIGIN OF FLIGHT, AND THE LEADING EDGE VORTEX

The year 1986 saw an amusing digression from Charlie’s main areas of interest. Prompted by a forthcoming symposium on biomechanics and evolution, he and I collaborated in investigating the vexed question of how insect flight evolved. There was general acceptance that wings arose from two pairs of a segmental series of lateral structures, but disagreement as to whether these were fixed or actively movable, and whether and how they could originally have functioned in gliding from trees. We investigated this by measuring the glide angle and speeds of a range of light balsa tubes with paired lateral ‘winglets’ whose angles of attack could be altered. Small models, corresponding to an insect about 25 mm long, glided steeply but stably, with
the winglets providing roll stability, and pitch stability if the posterior winglets were given an appropriate negative angle of attack. Yaw stability required a posterior filament to be attached. Removing the ‘abdominal’ plates while enlarging a ‘thoracic’ pair destroyed yaw stability, but this could be restored by attaching two oblique posterior filaments (see figure 6). We concluded (16) that the principal role of movable winglets would have been roll and pitch control, rather than lift enhancement. The experiments led Charlie to write the first proper aerodynamic analysis of the origin of insect flight (17).

Charlie’s research excellence was recognized in 1990 by the award of the Scientific Medal of the Zoological Society of London. By this time he was again focusing on novel aerodynamic mechanisms. Two new Cambridge graduates, James Wakeling and Alexander (Sandy) Willmott, began PhD research in his laboratory, the former comparing the kinematics, aerodynamics and energetics of two species of Odonata, the latter studying the dynamics of flight in the tobacco hornworm moth, *Manduca sexta*.

It was becoming increasingly clear from the bumblebee experiments and from work elsewhere (e.g. Cloupeau et al. 1979) that unsteady lift mechanisms were necessary for
forward flight as well as hovering; and these needed investigating. The various proposed mechanisms were still largely conjectural. Their evaluation would need precise information on the airflow past the wings and on the structure of the wake, and this would require the flow to be made visible. *Manduca*, which could be bred in the laboratory, had coupled wings like bees and superficially similar kinematics, and was the model of choice. For Willmott’s project, Charlie’s kinematic analysis software needed to be developed and refined to provide quantitative information on the wing shape and distribution of angle of attack along the span (29).

The moths flew, tethered in a way that allowed the insect to adjust its position and pitch and yaw and to support a significant proportion of its weight, in a wind tunnel at flow speeds from 0.4 to 5.7 m s\(^{-1}\). Stereophotography was used to record the flow of a rake of smoke filaments as they passed the insects. The results were remarkable. One of the possible unsteady mechanisms previously discussed had been ‘delayed stall’, a transient burst of high lift due to a short-lived vortex above the leading edge of an aerofoil when sharply accelerated at a high angle of attack. Though well known to aerodynamicists, this had previously been thought too brief to provide significant lift for insects before breaking away, but Willmott’s flow visualization clearly revealed a leading edge vortex that persisted and grew throughout the stroke, stabilized by spiralling outward along the span. The vortex was visible at all flight speeds, and grew larger as speed increased. The thesis and the three papers that resulted (27–29) earned Willmott the Thomas Henry Huxley Award of the Zoological Society of London.

In parallel, Charlie, with research assistant Adrian Thomas, who had played a significant role in the *Manduca* investigations, had built a splendid robotic insect, the ‘Flapper’; 10 times larger than *Manduca* and computer-controlled to simulate the latter’s hovering kinematics, with stroke frequency reduced to 0.3 Hz to preserve aerodynamic similarity. Tubes in the wings released smoke from the leading edge. The Flapper had its first public appearance (without smoke) at the Royal Society’s Soirées in 1995 (see figure 7).

When Coen van den Berg, a postdoctoral assistant from The Netherlands, began the experiment, the smoke injected above the leading edge behaved very like that in Willmott’s investigation, generating a similar leading edge vortex that travelled out along the span and merged into the tip vortex. Better still, further confirmation came from another source and another technique. At this time, Dr Keiji Kawachi at Tokyo University was leading a generously funded five-year government project on small-scale biological flight, and Charlie was invited to participate. He twice visited Tokyo for meetings with this group, one of whom, fluid dynamicist Shigeru Sunada, came to Cambridge to work in his laboratory. Charlie sent details of the *Manduca* kinematics to Hao Liu, a computational fluid dynamicist in Kawachi’s team. By the second visit in December 1995, Liu had generated a flow simulation that again clearly showed a leading edge vortex. I was with them in Tokyo and vividly remember our excitement when the results, arrived at by three different techniques, were brought together in Liu’s laboratory, in perfect agreement (figure 8). Delayed stall was now amply confirmed as a significant contributor to lift generation. This was particularly important for insects flying with a moderate stroke amplitude: most other unsteady mechanisms required the wings on the two sides to meet or closely approach each other at the top of the stroke, which is by no means always the case.

However, there was bad news. While dining with Kawachi and his wife on the last evening of the Tokyo visit, Charlie experienced a sharp chest pain. The return flight was booked and
imminent. We risked flying home, and he reached Cambridge safely, but suffered a serious heart attack in his GP’s surgery the following day and was immediately admitted to Papworth Hospital for a triple bypass.

He recovered well, but in retrospect this can be seen as the beginning of a long period of declining health, as diabetes progressively took its toll and other conditions arose. But his
career was then at its peak. In 1994, with Professor Tim Pedley (FRS 1995), he had organized and chaired an excellent Society for Experimental Biology Symposium on Biological Fluid Dynamics. His own paper in the volume was a valuable summary of the current state of play in insect unsteady aerodynamics, and included the first, brief, reference to the leading edge vortex (18). The *Manduca*/Flapper programme as a whole generated a letter in *Nature* in 1996 (19) and seven papers in front-line journals between 1996 and 1998 (20–22, 27–30). Wakeling’s dragonfly work led to three more (23–25).

Charlie was granted UK citizenship in 1995, was promoted to reader in animal mechanics in 1997 and was elected FRS in 1998 and to a chair of animal mechanics in 1999. In 1999, with John Altringham, he co-edited a tribute volume to Professor R. McNeill Alexander FRS, with a remarkable international array of distinguished contributors in all fields of biological biomechanics.

Ellington’s laboratory became a Mecca for overseas academics, some coming as postdoctoral associates, some as senior researchers on study leave. The latter included
Robert Josephson, an expert on muscle mechanics from the University of California at Irvine, and Johan van Leeuwen, leader of an outstanding biomechanics group at the University of Wageningen, Holland; both provided new skills and insights to the ongoing research.

With promotion, Charlie’s administrative workload, both internal and external, inevitably increased. He served on the advisory board for the Oxford University Press Animal Biology Series and the editorial boards of the *Journal of Experimental Biology*, *Physiological Zoology* and *Proceedings of the Royal Society B*. Fellowship of the Royal Society brought with it committee work and new responsibilities. Within Cambridge he was graduate tutor in Downing College and director of studies for undergraduates taking the biology component of the Natural Science Tripos, later succeeded by Stephanie (figure 9). He administered two Royal Society research funds, chaired the Mathematics Course Panel and the Safety Committee and had a succession of other roles and responsibilities in the Department of Zoology.

**THE NEW CENTURY**

Although aerodynamics had dominated the headlines in the 1990s, work in the lab on flight energetics and muscle physiology had continued, and would do so into the 2000s. Thomas Wolf worked for several years on the energetics of foraging bumblebees (11, 32). Robert
Josephson published with Charlie on power output in bumblebee flight muscle (26), and Graham Askew and R. L. Marsh with him on those of quail (33).

But the main occupation of the group continued to be fluid dynamics, and there was an unexpected development, bringing new incentives. In 1996 the US Department of Defense had expressed serious interest in the possibility of developing micro air vehicles (MAVs): tiny drones, primarily for surveillance in urban warfare. Substantial funding became available, and those of us working in insect flight found ourselves unexpectedly courted by the military and by robotics and control systems engineers seeking advice and collaboration. New groups entered the field, and research proliferated; for years afterwards almost every paper published stressed its possible relevance to MAVs, whether justified or not. As the senior worker in the field, Charlie was, of course, particularly in demand. His own contribution to the R. McNeill Alexander tribute volume was a seminal paper on the application of insect flight dynamics to MAVs (31), and in the following years he advised in several projects with the US Air Force and with Cranfield University. He co-organized conferences involving neurobiologists, aerodynamicists and roboticists in Brisbane in 2004 and Ascona in 2007. Ominously, ill health prevented him from attending both, and this was becoming increasingly frequent.

The leading edge vortex was established as a key component of unsteady lift generation in hawkmoths—but how universal was it? Over what size range did it operate? How much did wing shape matter? With the huge increase in available computing power and the development of digital imaging and laser lighting, new methods were appearing. Flow visualization with smoke was progressively being replaced by novel techniques: particularly particle image velocimetry (PIV), by which the instantaneous velocities of individual particles—usually tiny polymer flakes or oil droplets—could be computed and flow fields mapped with far greater precision than ever before.

Charlie began a project using PIV with the Flapper to investigate the effect of variations in wing design, but it failed to produce publishable results. A simple, typically Ellingtonian approach proved more productive. The base to tip velocity gradients of flapping could be simulated by revolving model wings around a central axis. Suitably instrumented to measure aerodynamic forces, and by introducing smoke to visualize flow, this could be used to explore the properties of model wings with different planforms, profiles and structural details, at different Reynolds numbers. Research student Jim Usherwood used this approach first to investigate first hawkmoth wings, and then to compare different insect wing shapes (34, 35).

Two particularly interesting results emerged. First, the leading edge vortex, while enhancing lift as expected, eliminated the ‘leading edge suction’ that counteracts drag in conventional aerofoils, so that drag was significantly increased. This would be bad in fixed or rotating aerofoils, but unimportant to flapping insects, which would simply manage the stroke plane so that the resultant of lift and drag was appropriately directed. Second, as the Reynolds number increased beyond the range in which insects operate, the leading edge vortex became destroyed by turbulence. This implied that there would be a size limit beyond which the LEV was useful, and called into question published reports that the vortex had been detected in birds. So far, Charlie had left the problems of vertebrate flight for others to solve, but he now became interested in comparing the flight of small birds with that of large insects. Hawkmoths in particular appear strikingly similar to hummingbirds when hovering, and are often confused by casual observers, but were the aerodynamics the same? With Douglas Altshuler and Robert Dudley, he applied the revolving wing method to hummingbird wings, which operate in the transitional zone between laminar and turbulent flow, and found that the aerodynamics were
significantly different: the LEV was absent, and the lift/drag ratio was far higher than in the moth (36). His last paper, with Yossef Elimelech, would use stereoscopic PIV to explore the flow field in detail over a hummingbird wing (38).

There was one more investigation on vertebrates in his group: how pterosaurian reptiles flew, and in particular what was the role of the unique pteroid bone in their wings. PhD student Matthew Wilkinson tested model pterosaur wings in a wind tunnel and found that if the pteroid was pointed forward, providing a leading edge flap, lift/drag ratios were greatly enhanced and lift was exceptionally high—suggesting that even the largest pterosaurs might have been able to take off and land without difficulty (37).

**RETIEMENT**

Charlie’s health had been seriously deteriorating throughout these last years, and he took early retirement in 2010. Graham Taylor, of the now very active Oxford University Flight Group, organized a retirement symposium for him in Cambridge, and researchers and friends came to the meeting from all over the world (figure 10).

Stephanie was now senior tutor at Lucy Cavendish College, Matthew was studying medicine at the University of Birmingham, and Nicholas was reading computer engineering at Bristol.

Charlie’s retirement was spent quietly at home in Woodditton, gardening, propagating plants from seed in the greenhouse, and cooking (and eating). In 2018 his health underwent rapid deterioration, and he was seriously ill in hospital for several months. Partly recovered, he spent six more months at home, but died peacefully on 30 July 2019. He lived to see Matthew in post as an anaesthetist at the Cambridge Deanery and Nicholas as an electronic trading strategist at Goldman Sachs. Happily, he had been able to attend Matthew’s wedding in June.

**ACHIEVEMENTS, AND PERSONAL QUALITIES**

Charlie Ellington was a fine scientist: an outstanding experimentalist and theoretician. His remarkable disciplinary breadth ideally equipped him to take advantage of the new technology of the 1970s to pioneer kinematic analysis of unimpeded insect flight and to provide a foundation for decades of research into animal aerodynamics and energetics in his own lab and elsewhere. His list of publications appears short by comparison with those of large present-day laboratories that produce 20 papers a year, but their quality is uniformly high, and some—the 1984 papers, the work with Dudley and with Machin and Casey on the flight energetics of bumblebees, and the cluster of papers on the leading edge vortex in the 1990s—rank among the most important in the whole field of animal flight.

Britain was lucky to keep him. Americans I met expressed surprise that he had not returned to the USA; but he much preferred Cambridge’s atmosphere of undemonstrative excellence to the fiercely competitive research world of the States—and Stephanie was in Cambridge. As a person, he combined quiet dignity with a lively sense of humour and a considerable sense of fun (see figures 4 and 10). He disliked ostentation and self-promotion—it is probably symbolic that when we exhibited together at the Soirées in 1995 he omitted to put our names on the display!
He was multi-talented: in his youth an excellent artist and illustrator, who also made metal sculptures; later highly competent at DIY and garden design. He was an excellent communicator, endlessly helpful in explaining difficult concepts to those—like myself—who struggled with them. As to teaching, the following abstract from the case for awarding him the Pilkington Prize says it all:

He manages to make quite difficult material ... not only understandable but also fun and entertaining to a wide range of biologists, for whom fun was probably very the last thing they expected ... In College, Charlie has been a highly valued supervisor and much-loved Director of Studies for generations of biologists ... [and] has made a substantial contribution to undergraduate teaching for over 30 years.

Most of his graduate students also held him in great affection—but a place in Charlie’s lab was no easy option. He was an absolute perfectionist, who expected the same high standards of research and behaviour as those he imposed on himself. Those who met these usually produced outstanding work, as evidenced by Sandy Willmott’s award and Alison Cooper’s high commendation for the Zoological Society’s Huxley Medal.
Type 1 diabetes affected his whole adult life. His physician in Maryland taught him how to regulate the condition, and it is greatly to his credit that Charlie survived, injecting daily, for nearly 50 years—far longer than anyone expected when it was first diagnosed. There were other problems: his heart attack, and a long period of incapacitating, undiagnosed neck pain in the 1990s, eventually corrected by operation. He coped with them all practically and philosophically, supported by his own inner resources and his deeply affectionate family. He is greatly missed.

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AUTHOR PROFILE

Robin Jeremy Wootton

Robin Jeremy Wootton, BSc PhD FLS Hon FRES, gained his BSc and PhD in Zoology at UCL when P. B. Medawar FRS 1949 was head of department. He then moved to the University of Exeter, where he remained throughout his career and is still an honorary research fellow. He was originally a palaeoentomologist, but, frustrated by the lack of functional thinking in the discipline, changed to insect flight mechanics at about the time that Charlie Ellington was beginning research at Cambridge. He and his students pioneered an engineering approach to insect wings using a combination of detailed morphology, mechanical testing, physical modelling and—originally advised by Weis-Fogh—free-flight high-speed cinematography. He stressed the unique role of insect wings as smart aerofoils that deform semi-automatically in flight, optimizing the airflow in response to the forces they receive. His research ran in parallel with, and complemented, Charlie Ellington’s aerodynamic studies and they were in close contact throughout their careers. He acted as examiner for several of Charlie’s postgraduate students. He and Charlie Ellington only published one joint paper, but they collaborated in organizing flight sessions at conferences and exhibited together at the Royal Society’s Soirées in 1995. He has written the obituaries for Charlie Ellington in the *International Journal of Odonatology* and, with Robert Dudley, in the *Journal of Experimental Biology*.

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