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OBITUARY

Charles Porter Ellington (1952–2019)

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By the mid-1970s, the study of insect flight mechanics was entering the doldrums. Two comprehensive papers in Journal of Experimental Biology by the Cambridge biologist Torkel Weis-Fogh had estimated quasi-steady lift and power requirements for a diversity of hovering taxa (Weis-Fogh, 1972, 1973), but mean force coefficients in some cases well exceeded those known to characterize airfoils at the relevant Reynolds numbers. The physical conundrum posed by Osborne (1951) in Journal of Experimental Biology (and harking back to pre-war studies) remained: how aerodynamically did bumblebees and many other volant taxa sustain their body weight?

Enter Charlie Ellington. A denizen of the eastern seaboard of the United States, and a graduate of Duke University where he worked with the influential biomechanicists Steve Vogel and Steve Wainwright, Charlie received in 1972 a Churchill Scholarship to study for a PhD at Cambridge University. Weis-Fogh quickly diverted Charlie from his original interest in fish swimming to work on insect flight. What ensued was a remarkable PhD dissertation that used high-speed cinematography, and novel methodology and software, to systematically analyse hovering kinematics, aerodynamics and energetics for a diversity of insect taxa. Critically, it was the first study to apply vortex theory to estimate circulation and associated lift production around flapping wings, together with the influence of the ensuing vortex wake, emphasizing the combined roles of wing rotation (as hypothesized by Weis-Fogh) and acceleration in generating the transient elevated forces necessary to support the body. The work was published in its entirety in an epic 1984 volume, with its six parts weighing in at 181 printed pages and additional plates, of the Philosophical Transactions of the Royal Society of London (Ellington, 1984a,b,c, d,e,f), dog-eared copies of which continue to grace many an animal flight laboratory around the world.

The approach taken by Charlie to hovering insect flight was systematic, starting with precise morphological characterization, and proceeding to the kinematic details of wing and body motions, aerodynamic calculations of ensuing forces, estimates of concomitant mechanical power expenditure and ultimately assessment of metabolic consequences. In aggregate, this linear approach formed the basis for numerous subsequent studies by others worldwide. One of us in Charlie's lab in the 1980s (R.D.) remembers the approach well ('Compute the Ellingtonian!'), as we envisaged a universal method for analysing the otherwise bewildering array of animal flight morphologies and behaviours. And although Charlie later trained a number of research students (19 in total) and 17 postdoctoral scholars, he wasn't really in a rush

Charlie and The Flapper, the latter making its first public appearance at the Royal Society Soirees in 1991. These events are full-dress affairs; it can just be seen that the flapper is wearing a bow tie. Photo credit: R.J.W.

to complete the administrative formalities of his own PhD. Cambridge nonetheless recognized his brilliance early on, appointing him first as a Research Assistant and then as a University Demonstrator well prior to the granting of a PhD in 1982. Charlie then became a University Lecturer, Reader in Animal Mechanics, and ultimately, in 1999, Professor of Animal Mechanics in the Department of Zoology.

Following his work on hovering mechanics, Charlie then pursued the question of forward flight in insects, employing the same analytical approach but for the first time measuring energetics directly for insects over a range of forward airspeeds. Using a custom-built closed-circuit wind tunnel, he and collaborators Tim Casey and Ken Machin measured rates of oxygen consumption for bumblebees and hoverflies over a range of forward airspeeds (Ellington et al., 1990). Amongst other technical innovations employed in this study, inflated condoms were used to equalize pressure between the sampled airstream and a reference air volume. Pipe in hand, Charlie once charitably commented that the exhortation of the 1980s era Thatcher administration to employ

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condoms actually had practical application! At the same time, Charlie productively entered into collaborations with one of us (R.J.W.) on the origins of insect flight, and with a number of other researchers on the physiology of asynchronous flight muscle. He was awarded the Scientific Medal of the Zoological Society in 1990.

But ultimately, Charlie's interests were aerodynamic, and in the mid-90s he innovated the mechanical flapper, a physically scaled-up but also slowed-down emulation of the wings of a hovering hawkmoth. At first glance a boffin-inspired device better suited for the Whipple Museum of the History of Science at Cambridge (see photo), the 'Flapper' combined realistic fluid dynamics with flow visualization, and was used to describe for the first time the leading-edge vortex of a moving wing at the Reynolds numbers relevant to flying animals (Ellington et al., 1996). Transiently high lift derived from the vortex, which tended to spiral but remain attached to the wing during the stroke via spanwise flow. This mechanism is now known to characterize the flight of many animals, and its discovery contributed in part to Charlie's 1998 election to fellowship of the Royal Society of London. Unsteady effects more generally are now well known to underpin high levels of force production on flapping wings, and to enable not just weight support but also transient forces and rotational moments that are the essence of aerial manoeuvrability.

Charlie's work at Cambridge University also included teaching and service responsibilities at Downing College in his role as Fellow, along with substantial contributions to Journal of Experimental Biology, the office of which was adjacent to his laboratory in later years. Charlie edited the journal from 1990 to 1994, assisted by the greatly missed Bob Boutilier. Contributors at that time will remember – and probably still treasure – their Christmas cards from that office, one showing Charlie, Bob and staff in ludicrous Yuletide costumes, and another a spoof edition of Journal of Experimental Biology with a convincing cover and a full table of contents featuring familiar authors and just-plausible titles. Legend has it that some recipients entirely missed the joke, and sent puzzled letters asking for the missing pages, which were otherwise represented by blocks of expanded polystyrene.

Charlie was seriously diabetic from childhood, and in the 1990s his health began to deteriorate. He continued to supervise students; a number of leading scientists from Europe, USA and Japan also visited his laboratory to work, collaborate and publish with him. He took early retirement in 2010, and a symposium was held in Cambridge in his honour, attended by former students, colleagues and friends from around the world. Thereafter, he lived quietly with his wife Stephanie in a village near Newmarket, while their two sons, Matt and Nick, began successful careers. In 2018 his health underwent rapid deterioration, and he was seriously ill in hospital for several months. Partly recovered, he then spent six more months at home, but died peacefully on 30 July 2019. His intellectual presence in and contributions to the field of animal flight mechanics will be sorely missed.

References

Ellington, C. P. (1984a). The aerodynamics of hovering insect flight. I. The quasi-steady analysis. *Phil. Trans. R. Soc. Lond. B* **305**, 1-15. doi:10.1098/rstb.1984.0049

Ellington, C. P. (1984b). The aerodynamics of hovering insect flight. II. Morphological parameters. *Phil. Trans. R. Soc. Lond. B* **305**, 17-40. doi:10.1098/rstb.1984.0050

Ellington, C. P. (1984c). The aerodynamics of hovering insect flight. III. Kinematics. *Phil. Trans. R. Soc. Lond. B* **305**, 41-78. doi:10.1098/rstb.1984.0051

Ellington, C. P. (1984d). The aerodynamics of hovering insect flight. IV. Aerodynamic mechanisms. *Phil. Trans. R. Soc. Lond. B* **305**, 79-113. doi:10.1098/rstb.1984.0052

Ellington, C. P. (1984e). The aerodynamics of hovering insect flight. V. A vortex theory. *Phil. Trans. R. Soc. Lond. B* **305**, 115-144. doi:10.1098/rstb.1984.0053

Ellington, C. P. (1984f). The aerodynamics of hovering insect flight. VI. Lift and power requirements. *Phil. Trans. R. Soc. Lond. B* **305**, 145-181. doi:10.1098/rstb.1984.0054

Ellington, C. P., Machin, K. E. and Casey, T. M. (1990). Oxygen consumption of bumblebees in forward flight. *Nature* **347**, 472-473. doi:10.1038/347472a0

Ellington, C. P., van den Berg, C., Willmott, A. P. and Thomas, A. L. R. (1996). Leading-edge vortices in insect flight. *Nature* **384**, 626-630. doi:10.1038/384626a0

Osborne, M. F. M. (1951). Aerodynamics of flapping flight with application to insects. *J. Exp. Biol* **28**, 221-245.

Weis-Fogh, T. (1972). Energetics of hovering flight in hummingbirds and in *Drosophila*. *J. Exp. Biol* **56**, 79-104.

Weis-Fogh, T. (1973). Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift production. *J. Exp. Biol* **59**, 169-230.