

CLASSICS

Eppur si vola (and yet it flies)



Sanjay Sane discusses the impact of Charles Ellington's classic series of papers, 'The aerodynamics of hovering insect flight' parts I–VI, published in *Philosophical Transactions of the Royal Society of London* in 1984.

In his book *'Le Vol des Insectes'*, which was published in 1934, the French entomologist Antoine Magnan mentioned in passing that when he and his assistant, the mathematician André Sainte-Laguë, applied the conventional laws of fixed-wing aerodynamics to flapping wings, they were unable to explain how insects could fly (Magnan, 1934). Thus was born the infamous 'bumblebee paradox', much to the annoyance of many future generations of insect flight researchers (McMasters, 1989). Yet, at the core of this myth was a genuine problem: the principles of fixed wing flight did indeed come up short in predicting how insects could offset their body weight during flight. This question formed the basis of Charles P. Ellington's seminal six paper opus in 1984, entitled 'The aerodynamics of hovering insect flight', parts I–VI, which occupied a whole issue of the *Philosophical Transactions of the Royal Society of London* (Ellington, 1984a,b,c,d,e,f).

Ellington was a young American graduate student in Torkel Weis-Fogh's laboratory at the University of Cambridge, UK. Weis-Fogh had recently conducted an expansive survey of wing movements in diverse flying insects using state-of-the-

art high-speed cinematography (Weis-Fogh, 1973). Having already made several pioneering discoveries in organismal biology, Weis-Fogh turned his attention to the physical and neural basis of insect flight (e.g. Sane, 2011). His laboratory was a premier centre for studies on all aspects of insect flight, ranging from physics to physiology. This exhaustive survey led Weis-Fogh to suggest a theoretical framework called 'the steady-state paradigm' (later retooled as the quasi-steady paradigm) in which the moving wing could be viewed as a series of instantaneous 'snapshots'. In each snapshot, the wing position and attitude were assumed to be static relative to a steady ambient flow. The whole kinematic sequence of the moving wing could then be viewed as a time series of static states, each experiencing a steady force that depends only on its instantaneous state. From this sequence, a time series of forces could be reconstructed; however, it did not incorporate the history-dependent effects, such as those due to a vortex that changes its strength with time. From his investigations, Weis-Fogh concluded that the steady-state (or quasi-steady) paradigm could reasonably predict the aerodynamic forces on a flapping wing. In other words, the bumblebee paradox was an anomaly in a few insects, but unnecessary for most others.

In cases where the quasi-steady theory failed, there must be specific unsteady mechanisms that aid in enhancing lift. One such mechanism was the clap-and-fling, a novel aerodynamic mechanism that Weis-Fogh proposed for enhanced lift generation in certain small flying insects (Weis-Fogh, 1973). This mechanism caught the attention of the foremost fluid mechanists of the time, Sir James Lighthill (Lighthill, 1973), but it was by no means generally explanatory of the bumblebee paradox because very few insects displayed clap-and-fling. This meant that there were other unsteady mechanisms that needed to be discovered. Given the depth of knowledge in aerodynamics of fixed-wing flight, it was hard for aerodynamicists to fathom what could possibly be still left undiscovered.

The discovery of clap-and-fling was greeted with excitement because it was a completely new mechanism. Perhaps insects offered more solutions that had eluded aeronautics engineers.

Following Weis-Fogh's tragic death in 1975, the task of synthesizing the many loose ends of this survey into a coherent set of ideas and observations fell on the shoulders of the young Ellington. Much of what is published in 'the Ellington, 1984 papers' (as they are often referred) emerges from his broad-ranging survey of flying insects in which he not only re-examined the quasi-steady theory but also proposed a complete overhaul of the theoretical set-up, and laid down the basic mathematical language and concepts that were necessary for such studies. Not surprisingly, the Ellington papers became absolutely indispensable for all future studies on the physics of insect flight.

How was this opus constructed? In the first of his six-part monograph (Ellington, 1984a), Ellington invoked the logical construct of 'proof-by-contradiction' to put the quasi-steady theory to a rigorous test. He argued that if the mean lift required to hover was greater than the maximum lift predicted by the quasi-steady model, then the model was insufficient. However, if the maximum force calculated from the model exceeded or equalled the mean forces for hovering, then the quasi-steady model remained unfalsified. When the available data from the broad survey were put to this litmus test, it came up short, thus reprising the bumblebee paradox. This meant that the existing theory needed to be revised to explain how insects generate sufficient forces for flight.

Ellington focused the next two parts on describing in great detail the morphology (Ellington, 1984b) and kinematics (Ellington, 1984c) of wings during flight, as well as the methodological details for filming flying insects and reconstructing their kinematics. He established standard procedures for comparing the wing shapes of all insects ranging in size from a few millimetres to tens of centimetres, by accounting for their dimensions. This process, called 'non-dimensionalization',

Classics is an occasional column, featuring historic publications from the literature. These articles, written by modern experts in the field, discuss each classic paper's impact on the field of biology and their own work.

is just one of many procedures laid down in these papers that have been embraced by the entire field as an ‘industry standard’. Although mostly descriptive, these papers were certainly not lacking in surprises. For instance, when Ellington plotted the dimensionless higher-order distributions (or moments) of wing area against wing mass or virtual mass due to accelerative effects, there emerged extraordinarily tight correlations which he was unable to explain using any available concepts. He called these relationships the ‘laws of shape’, hinting at some underlying evolutionary scaling rules (Ellington, 1984b). Even three decades later, these relationships remain remarkably unexplored and scientifically fresh.

What makes the above two descriptive papers special is the deep scholarship and their strongly comparative flavour. While being able to synthesize the broader information into concepts such as the laws of shape, these papers also provided ready reference tables for specific values on specific insects that made them an essential resource for later studies. I have lost track of the number of times that I have had to say, ‘Look up Ellington II/III’, whenever students asked me questions about the wing morphology or shape of a specific insect wing, or the kinematics of their movement.

Having dealt with the descriptive aspects pertaining to flight, Ellington then focused his attention on the core topic of aerodynamics of flight in part IV (Ellington, 1984d). He first elucidated the basic elements of quasi-steady theory and the various known unsteady (i.e. history-dependent) effects. He drew extensively from all available sources of information on insect flight aerodynamics and applied them to the data in diverse insects. In doing so, he had to refer to literature well beyond the conventional boundaries of a biological study, to include concepts from helicopter and aerofoil theory. Based on these investigations, he concluded that the existing quasi-steady theory, when applied to insect flight, was insufficient and perhaps incomplete. To complete it required the inclusion of the aerodynamic effects of wing rotation at the end of each stroke and Ellington again made specific recommendations. It also required inclusion of specific history-dependent effects such as the Wagner effect, in which the forces generated by an aerofoil

are influenced by its proximity to a vortex that has just been shed, or the clap-and-fling in which the proximity of two aerofoils to each other affects their aerodynamic forces.

Next, in part V, Ellington proposed a completely new theoretical structure, called the ‘vortex theory’ in which he used averaged flow parameters around a flapping wing to deduce lift (Ellington, 1984e). This theory was inspired by the helicopter or propeller (or Rankine–Froude) theory, in which a steadily rotating propeller could be idealized into an ‘actuator disc’ – a pulsating disc that generated periodic momentum pulses, not unlike those generated by the flap of every wing. A similar theory was developed in parallel by Jeremy Rayner for birds (Rayner, 1979a,b), and Ellington made explicit comparisons between Rayner’s theory and his own. For the most part, the two theories agreed with each other, which was not surprising, because their basic assumptions were similar. However, there were minor differences which Ellington pointed out, mostly due to different assumptions for birds versus insects. Both theories focused on averaged wakes rather than instantaneous forces, which greatly constrained their scope. Nevertheless, they served as a source of inspiration for several studies on both avian and entomological flight in subsequent decades. They were particularly useful for field-based studies in which detailed wing kinematics were not easy to acquire.

In the final paper in this series, Ellington applied these ideas to derive quantities, such as power, efficiency and elastic storage, to bridge the gap between physics and physiology (Ellington, 1984f). He presented an accounting scheme for mechanical power as the sum of aerodynamic and inertial power. This scheme was strongly grounded in measurements and experiments, with aerodynamic power being divided into induced, profile and parasite power. Much of aerodynamic theory comes to bear in deriving these quantities from reconstructions of wing movements and morphological measurements. This made paper VI a particularly useful reference for researchers studying the role of flight muscles and energetics.

Collectively, these papers completely transformed the field of insect flight. They

provided a common language that could be understood by biologists as well as aeronautical engineers. Ellington struck a very fine balance between mathematical rigour on the one hand and comparative approach on the other; these papers are as useful to taxonomists wondering about how wing shape changes from one order of insects to another, as they are to aerodynamicists who wish to model the forces on a flapping wing of any shape. This 1984 issue of *Philosophical Transactions of the Royal Society of London* rapidly became a must-read for all students of the topic. My PhD advisor owned a bound, much-battered and coffee-stained copy filled with many scribbles in the margins. My own copy has suffered a similar fate, and is one of my most prized possessions. It is a staggering fact that this was Ellington’s graduate work, for which he received a PhD in 1982.

In the decades following the publication of the Ellington papers, the insect flight problem became a paradox no more (Sane, 2003). In the mid-1990s, detailed studies on smoke flows around insect wings by Ellington and his colleagues led to the discovery of the leading edge vortices, and a large piece of the insect flight puzzle fell into place (Ellington et al., 1996). Through the efforts of many international research teams, this question now stands experimentally resolved and the forces on insect wings can be analytically calculated using the quasi-steady model (Sane and Dickinson, 2002) or computationally solved using full Navier–Stokes solvers (Liu and Kawachi, 1998; Liu et al., 1998; Sun and Tang, 2002). The flows around flapping wings can be simulated by computational methods or visualized using state-of-the-art particle image velocimetry techniques in both models (Lehmann et al., 2005) and real insects (Bomphrey, 2006). Much of the focus now is on using these principles to develop small flapping robots that are inspired by insects, or to understand other aspects of flight as it relates to ecology or neurobiology. The Ellington 1984 papers are undoubtedly the centrepiece of all these achievements and continue to guide our thinking on these topics.

Sanjay P. Sane
National Centre for Biological Sciences,
Tata Institute of Fundamental Research
sane@ncbs.res.in

References

- Bomphrey, R. J.** (2006). Insects in flight: direct visualization and flow measurements. *Bioinspir. Biomim.* **1**, S1-S9.
- 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.
- Ellington, C. P.** (1984a). The aerodynamics of hovering insect flight. I. The quasi-steady analysis. *Philos. Trans. R Soc. Lond. B Biol. Sci.*, **305**, 1-15.
- Ellington, C. P.** (1984b). The aerodynamics of hovering insect flight. II. Morphological parameters. *Philos. Trans. R Soc. Lond. B Biol. Sci.* **305**, 17-40.
- Ellington, C. P.** (1984c). The aerodynamics of hovering insect flight. III. Kinematics. *Philos. Trans. R Soc. Lond. B Biol. Sci.* **305**, 41-78.
- Ellington, C. P.** (1984d). The aerodynamics of hovering insect flight. IV. Aerodynamic mechanisms. *Philos. Trans. R Soc. Lond. B Biol. Sci.* **305**, 79-113.
- Ellington, C. P.** (1984e). The aerodynamics of hovering insect flight. V. A vortex theory. *Philos. Trans. R Soc. Lond. B Biol. Sci.* **305**, 115-144.
- Ellington, C. P.** (1984f). The aerodynamics of hovering insect flight. VI. Lift and power requirements. *Philos. Trans. R Soc. Lond. B Biol. Sci.* **305**, 145-181.
- Lehmann, F.-O., Sane, S. P. and Dickinson, M.** (2005). The aerodynamic effects of wing-wing interaction in flapping insect wings. *J. Exp. Biol.* **208**, 3075-3092.
- Lighthill, M. J.** (1973). On the Weis-Fogh mechanism of lift generation. *J. Fluid Mech.*, **60**, 1.
- Liu, H. and Kawachi, K.** (1998). A numerical study of insect flight. *J. Comput. Phys.* **146**, 124-156.
- Liu, H., Ellington, C. P., Kawachi, K., van den Berg, C. and Willmott, A. P.** (1998). A computational fluid dynamic study of hawkmoth hovering. *J. Exp. Biol.* **201**, 461-477.
- Magnan, A.** (1934). *Le Vol des Insectes*. Paris: Hermann.
- McMasters, J. H.** (1989). The flight of the bumblebee and related myths of entomological engineering: bees help bridge the gap between science and engineering. *Am. Sci.* **77**, 164-169.
- Rayner, J. M. V.** (1979a). A vortex theory of animal flight. Part 1. The vortex wake of a hovering animal. *J. Fluid Mech.* **91**, 697.
- Rayner, J. M. V.** (1979b). A vortex theory of animal flight. Part 2. The forward flight of birds. *J. Fluid Mech.* **91**, 731-763.
- Sane, S. P.** (2003). The aerodynamics of insect flight. *J. Exp. Biol.* **206**, 4191-4208.
- Sane, S. P.** (2011). Steady or unsteady? Uncovering the aerodynamic mechanisms of insect flight. *J. Exp. Biol.* **214**, 349-351.
- Sane, S. P. and Dickinson, M. H.** (2002). The aerodynamic effects of wing rotation and a revised quasi-steady model of flapping flight. *J. Exp. Biol.* **205**, 1087-1096.
- Sun, M. and Tang, J.** (2002). Unsteady aerodynamic force generation by a model fruit fly wing in flapping motion. *J. Exp. Biol.* **205**, 55-70.
- Weis-Fogh, T.** (1973). Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift production. *J. Exp. Biol.* **59**, 169-230.