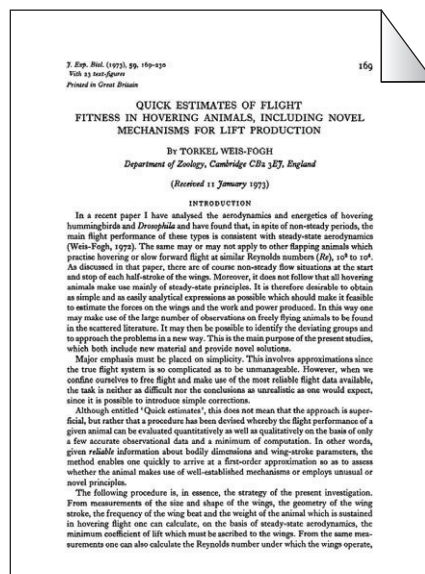


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# JEB CLASSICS

## STEADY OR UNSTEADY? UNCOVERING THE AERODYNAMIC MECHANISMS OF INSECT FLIGHT



Sanjay Sane discusses Torkel Weis-Fogh's paper entitled 'Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift production'.

A copy of the paper can be obtained from <http://jeb.biologists.org/cgi/content/abstract/59/1/169>

As in art or music, classic works in science can often be identified by the new research directions they stimulate. Some papers become classics by virtue of specific findings that fundamentally alter our understanding of a topic, while others provide a philosophical roadmap that makes clear the way forward in that subject. By both these criteria, Torkel Weis-Fogh's *Journal of Experimental Biology* 1973 paper holds a very special place in the study of insect flight (Weis-Fogh, 1973).

Weis-Fogh was already widely recognized for his ground-breaking discoveries in comparative biology in the three decades preceding this paper. On the biomechanics front, he had discovered and physically characterized an elastic element in the locust tendon called resilin, which remains the most efficient rubber protein studied to date (Weis-Fogh, 1960) (see also Bennet-Clark, 2007). He had also studied the molecular basis of the long-range elasticity of elastin, the vertebrate equivalent of resilin (Weis-Fogh and Andersen, 1970). In sensory neurobiology, he had shown that cephalic bristles in insects play an important mechanosensory role in the detection of air flow (Weis-Fogh, 1949). In cell mechanics, he had discovered a novel calcium-dependent contractile mechanism

in the intracellular fibres (or spasmonemes) of protozoan vorticellid ciliates that powers the contraction of their stalks (Weis-Fogh and Amos, 1972). Because these discoveries were primarily experimental in nature, the techniques pioneered by Weis-Fogh helped launch several research programmes in their own right. For example, it was in Weis-Fogh's laboratory that Don Wilson first discovered the central pattern generators in flying locusts (see Edwards, 2006; Wilson, 1961). Nevertheless, Weis-Fogh's 1973 paper remains his most cited and, arguably, his most influential work.

To fully appreciate the importance of this paper, it is necessary to understand its historical underpinnings. On the heels of the development of the modern aircraft in the early twentieth century, scientists turned their eye to the flight of smaller 'natural' aircrafts such as insects. Could one explain their flight using the conventional theory that was developed mainly for large aircrafts, or was it necessary to invoke non-conventional mechanisms to understand flight force generation in these animals? Unfortunately, these initial attempts at using conventional airfoil theory, although effective in understanding airplane aerodynamics, failed to predict the forces generated by flapping insect wings. There was a growing feeling that unconventional mechanisms of lift generation must be important in insect flight. This posed a major challenge to physicists and engineers who wished to understand how insects generate flight forces, and also biologists working on diverse questions relating to sensorimotor physiology, flight muscle function, metabolic rates and energetics of insect flight.

It was from an energetics view point that a young Weis-Fogh began his studies of locust flight in the laboratory of the Nobel Prize-winning Danish comparative physiologist August Krogh. In Krogh's laboratory, he collaborated with Martin Jensen (Weis-Fogh, 1956; Weis-Fogh and Jensen, 1956) to study the aerodynamics of insect flight. After reviewing the existing literature on the topic, they concluded that conventional airfoil theory was perhaps adequate but the lack of data on wing motion in insects meant that the subtleties of wing morphology and kinematics were not properly incorporated into the theoretical framework to calculate flight forces. To address this problem, they developed a heuristic framework to rigorously account for the kinematics and morphology of flapping insect wings in the aerodynamics and energy calculations, and showed that, at least in the case of locusts, it was not necessary to invoke

unconventional methods of lift generation. It remained to be seen, however, whether these conclusions held for other insects.

After moving to the University of Cambridge, Weis-Fogh embarked on a broad survey of insects with the aim of formulating a general theory of insect flight. This survey involved the use of high-speed cinematography to quantify insect wing kinematics combined with a detailed morphometric study of their wings and bodies. He could now compare tiny insects, which flew under a relatively viscous-driven low Reynolds number (which is the non-dimensional ratio of inertial to viscous forces in a fluid) regime, with large insects, birds and bats, which operated at higher, more inertia-driven Reynolds numbers. Weis-Fogh focused on hovering or slow-flying insects for which the lift force exactly offsets body weight. The focus on hovering also ensured that history-related effects were maximal and his conclusions more conservative.

To summarize the lessons of this survey, it was necessary to generate a simple set of mathematical formulae that scaled well for size and Reynolds number regimes. However, for such a formula to work, it was crucial to hypothesize that common physical principles of force generation operated at all size scales. As a trial run to test this hypothesis, Weis-Fogh compared the hovering flight of small fruit fly, *Drosophila virilis*, with that of the larger hummingbird, *Amazilia fimbriata* (Weis-Fogh, 1972). For this purpose, Weis-Fogh developed a paradigm called the ‘steady-state principle’ (also called the ‘quasi-steady principle’) according to which the instantaneous forces generated by the wings were independent of the history of the flows caused by the wing’s prior motion. He found that despite large differences in Reynolds numbers of these two flight systems, the steady-state model satisfactorily described both cases. Thus, as in locusts, which operated at intermediate Reynolds numbers, it seemed unnecessary to invoke unsteady mechanisms to calculate their flight forces.

For the broader survey reported in the 1973 paper (Weis-Fogh, 1973), Weis-Fogh then presented the following logical criterion to test whether the steady-state approach was worth pursuing: in hovering insects, it is possible to estimate from the wing kinematics, wing geometry and body weight how much minimum lift is required from the wings to satisfy the steady-state model. From the same set of input conditions, we may also calculate the Reynolds numbers and how much maximum lift to expect from the wings at

these Reynolds numbers. If the minimum lift required by the steady-state model is within the range of what can be obtained at these Reynolds numbers, then the steady-state model cannot be discounted. However, if the minimum lift required by the steady-state model is beyond the range of what can be obtained at these Reynolds numbers, then the steady-state model is clearly insufficient. In either case, one cannot entirely rule out the presence of unsteady mechanisms – the only question is their relative importance compared with steady-state mechanisms. To widen the scope of his survey, Weis-Fogh extended the range of Reynolds numbers at both ends to now include the extremely tiny chalcid wasp *Encarsia formosa* with Reynolds numbers of the order of 10, to large beetles, bats and birds with Reynolds numbers of the order of  $10^4$ . Weis-Fogh’s broad conclusion from this major exercise was that, for most insects, the steady-state model was adequate and one could, after all, derive general formulae to study the energetics and physiology of insect flight in most cases. It is impossible to overstate the importance of this conclusion for the vast majority of researchers, who would no longer need to worry about the specific aerodynamic mechanisms operating in their research animal. Instead, they could simply

adapt Weis-Fogh’s formulae for their system with only the prior knowledge of morphometrics (often obtainable even from museum specimens) and a few simple kinematic and aerodynamic estimates.

Weis-Fogh noticed that in a few cases such as *E. formosa*, the steady-state model failed. This set him on a course to determine the unsteady fluid mechanisms that enabled high lift generation well beyond the values predicted by the steady-state model. In this search, he was aided by one of the foremost fluid mechanics investigators of his time, the late Sir James Lighthill, also from Cambridge University. From his discussions with Lighthill, Weis-Fogh had learnt of a peculiar unsteady fluid dynamic phenomenon called the Wagner effect, which was known to cause a history-dependent delay in the generation of lift. The Wagner effect occurs when an inclined wing moves impulsively, shedding in its wake a counter-vortex from its trailing edge. In the initial stages of the shedding, the counter-vortex is in close physical proximity to the wing, thereby inducing a delay in the lift generation. Under the more viscous low Reynolds number conditions in which *E. formosa* operates, this delay should be accentuated. How then does it generate high lift when it should be fighting

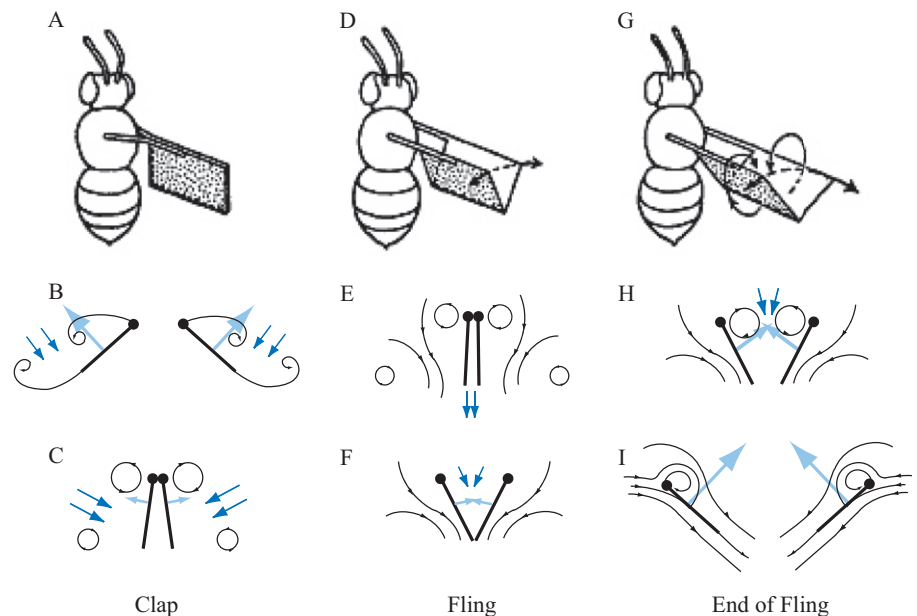


Fig. 1. Top row, Weis-Fogh’s illustration of the clap-and-fling mechanism from his 1973 paper. (A–C) Clap mechanism: prior to dorsal stroke reversal, as the wings come together and join (A), they carry with them leading and trailing edge vortices and wakes (B,C) which attenuate each other due to their mutually opposite sense. (D–F) Fling mechanism: as the wings fling apart (D), fluid is sucked into the widening cleft between the wings, thus helping initiate circulation around each wing (E,F). (G,H) End of fling: as the wings move apart, each wing generates a leading edge vortex. However, the trailing edge vortices from each wing are of the opposite sense and hence nullify each other (G,H). Under these circumstances, a wing can begin impulsively in the absence of the trailing edge vorticity thereby avoiding the slow rise in circulation and lift generation. Bottom two panels are reprinted from a recent review (Sane, 2003) to illustrate a more modern view of the flap-and-fling mechanism. Reproduced with permission (Weis-Fogh, 1973; Sane, 2003).

the Wagner effect through most of its stroke?

Weis-Fogh had noticed that the wings of *E. formosa* and a few other insects came in close apposition to one another at the dorsal stroke reversal, thus performing a 'clap'. When these wings 'flung' apart in a symmetrical fashion at the onset of the following stroke, their starting vortices exactly annihilated one another as they were of opposite sense. Because the absence of a starting vortex also meant no Wagner effect, lift could be generated without any delay, thus enhancing the average lift over the entire stroke. This so-called 'clap and fling effect' (or eponymously 'Weis-Fogh effect') came as an exciting surprise to a generation of aerodynamicists, who always assumed that the cost of counter-vorticity was unavoidable (Fig. 1). Following Weis-Fogh's suggestion, Lighthill worked out the theoretical details of the Weis-Fogh effect and confirmed that his intuition was indeed accurate (Lighthill, 1973).

The paper contains numerous other equally important observations, which are less well detailed. For instance, Weis-Fogh noticed that, in most insects, the inertial forces are relatively more important than aerodynamic forces by a factor of 2–3. This means that, in the absence of an elastic storage system, insects would need to spend most of their mechanical energy on moving the mass of their wings rather than generating aerodynamic forces. Thus, elastic storage elements such as resilin, are needed to ensure energetically efficient flight. Another key insight involves the aerodynamic importance of the 'flip' mechanism which occurs at the onset of the upstroke (as well as the downstroke in several cases) when the wings rapidly undergo a large angular twist. Weis-Fogh speculated that the flip may be involved in jump-starting the force generation for that stroke, an observation that was later confirmed by Dickinson and colleagues (Dickinson et al., 1999).

Sadly, this was Weis-Fogh's final research report on insect flight and one written in a phase of great personal turmoil in his life. His wife, Hanne Weis-Fogh (to whom this paper is dedicated), was killed in a car accident that also left Weis-Fogh severely

injured. Neither his body nor his mind fully healed from this tragedy, and he committed suicide on 13th November, 1975. However, the momentum provided to the field by his 1973 paper continued unabated. Weis-Fogh's findings and ideas received a most thorough critical review in the works of Charles Ellington (Ellington, 1984) who, after comprehensively re-examining all available literature and data in the field, reached the conclusion that a steady-state approach was insufficient at least from the measurements available at the time. He also emphasized the need to incorporate near-field flows to address mechanisms of force generation as the measurement and visualization of flows remained the one missing piece in the elaborate and formidable edifice that Weis-Fogh constructed in his 1973 paper.

Scientific ideas often return in cycles. In the decade following Weis-Fogh's 1973 paper, a key piece of the puzzle was solved with the observation by Ellington and co-workers (and several groups since) of a leading-edge vortex that remained stable and sustained through the entire stroke even at high angles of attack (Ellington et al., 1996). Thus, the three-dimensional flow patterns around flapping wings were fundamentally different from those around fixed wings, and hence the force coefficients measured on fixed wings placed in wind tunnels would underestimate the lift generated during flight. Complimenting these observations were force measurements that demonstrated the constancy of the flows (and forces) around a flapping wing, and thus the unimportance of the history-related effects. Armed with these new data, it was again reasonable to expect that the steady-state model should predict both mean and instantaneous forces around flapping wings provided the forces were measured on flapping rather than fixed wings (Dickinson et al., 1999; Sane, 2003). These later studies made use of dynamically scaled mechanical models to measure the forces and flows on flapping wings. There have been numerous studies on the aerodynamics of insect flight over the past two decades – far too many to mention here – that have employed state-of-the-art computational fluid dynamics and digital flow visualization techniques to rigorously address the connection between

flows, forces, pressure distribution on the wing, work, power and energetics. Many of these have also used new approaches to study the phenomena that Weis-Fogh describes in his paper (e.g. Lehmann et al., 2005; Miller and Peskin, 2005; Spedding and Maxworthy, 1986). It would be hardly unfair to describe these researches as the progeny of Weis-Fogh (Weis-Fogh, 1973).

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## References

- Bennet-Clark, H. (2007). The first description of resilin. *J. Exp. Biol.* **210**, 3879–3881.
- Dickinson, M. H., Lehmann, F. O. and Sane, S. P. (1999). Wing rotation and the aerodynamic basis of insect flight. *Science* **284**, 1954–1960.
- Edwards, J. S. (2006). The central nervous control of insect flight. *J. Exp. Biol.* **209**, 4411–4413.
- Ellington, C. P. (1984). The aerodynamics of hovering insect flight. 1. The quasi-steady analysis. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* **305**, 1–15.
- 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.
- 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. (1973). On Weis-Fogh mechanism of lift generation. *J. Fluid Mech.* **60**, 1–17.
- Miller, L. A. and Peskin, C. S. (2005). A computational fluid dynamics of 'clap and fling' in the smallest insects. *J. Exp. Biol.* **208**, 195–212.
- Sane, S. P. (2003). The aerodynamics of insect flight. *J. Exp. Biol.* **206**, 4191–4208.
- Spedding, G. R. and Maxworthy, T. (1986). The generation of circulation and lift in a rigid two-dimensional fling. *J. Fluid Mech.* **165**, 247–272.
- Weis-Fogh, T. (1949). An aerodynamic sense organ stimulating and regulating flight in locusts. *Nature* **164**, 873.
- Weis-Fogh, T. (1956). Biology and physics of locust flight. 2. Flight performance of the desert locust (*Schistocerca gregaria*). *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* **239**, 459–510.
- Weis-Fogh, T. (1960). A rubber-like protein in insect cuticle. *J. Exp. Biol.* **37**, 889–907.
- 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.
- Weis-Fogh, T. and Amos, W. B. (1972). Evidence for a new mechanism of cell motility. *Nature* **236**, 301–304.
- Weis-Fogh, T. and Andersen, S. O. (1970). New molecular model for long-range elasticity of elastin. *Nature* **227**, 718–721.
- Weis-Fogh, T. and Jensen, M. (1956). Biology and physics of locust flight. 1. Basic principles in insect flight – a critical review. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* **239**, 415–458.
- Wilson, D. M. (1961). Central nervous control of flight in a Locust. *J. Exp. Biol.* **38**, 471–490.