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DISCUSSION

# Beyond robins: aerodynamic analyses of animal flight

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Recent progress in studies of animal flight mechanics is reviewed. A range of birds, and now bats, has been studied in wind tunnel facilities, revealing an array of wake patterns caused by the beating wings and also by the drag on the body. Nevertheless, the quantitative analysis of these complex wake structures shows a degree of similarity among all the different wake patterns and a close agreement with standard quasi-steady aerodynamic models and predictions. At the same time, new data on the flow over a bat wing in mid-downstroke show that, at least in this case, such simplifications cannot be useful in describing in detail either the wing properties or control prospects. The reasons for these apparently divergent results are discussed and prospects for future advances are considered.

**Keywords: animal flight; aerodynamics; flow visualization**

## 1. ANALYSIS AND MODELLING OF ANIMAL FLIGHT

The intricate kinematics and complex time-varying geometries of animal wings in flapping flight seem to raise daunting challenges to any realistic aerodynamic analysis. However, just as the rapid progress in aeronautics was assisted by the development and use of simplified empirical and analytical models, so certain aspects of these models can be adapted to animal flight with surprising success.

Consider a bird in flapping flight that supports its weight, $W$, by generating the required lift, $L$, from the aerodynamic forces on the wings. (The wing flapping motion also allows the bird to produce a thrust, $T$, that balances the total drag, $D$, on the wings and the body.) Newton's third law requires that the forces exerted by the air upon the bird must be equal and opposite to those exerted by the wings and the body upon the air, and so the air motions themselves contain a record of the magnitude and time history of these forces. In principle, the analysis of these wakes allows the forces to be deduced without ever touching the bird itself, which is otherwise allowed to fly freely.

The wake motions themselves can often be described economically by distributions of vorticity, where the global properties of the airflow can be modelled as being induced by a small number of line vortices (or similar convenient mathematical objects) around which the flow circulates. The strength of the vortex elements indeed can be calculated from the integrated magnitude of the vorticity distributions, which is termed the circulation, $\Gamma$. This analytical framework combines in a powerful way with a classical aerodynamics theorem stating that the lift per unit span, $L'$, of a wing moving at a uniform speed, $U$, in a fluid of density $\rho$ depends only on the product of these quantities with a 'bound circulation' that represents the effect of the aerofoil on the flow,

$$L' = \rho U \Gamma. \tag{1.1}$$

A further theorem by Kelvin proves that, in a uniform fluid, circulation ($\Gamma$) can be neither created nor destroyed (it is a conserved quantity); therefore, the only way for some finite value of $\Gamma$ to appear in equation (1.1) is for an equal and opposite amount to be deposited in the surrounding fluid, so that the net sum remains zero. Therefore, variations in $\Gamma$ in the wake can be related to variations in $\Gamma$ on the wing, which are directly related (through equation (1.1)) to variations in the lift force on the wing.

In the early development of vortex models of animal flight (Ellington 1978; Rayner 1979*a*,*b*), it was realized that focusing on the wake dynamics rather than on the complex motions of the solid body that creates it could produce tractable and predictive models that did not depend on every detail of the wake generator itself. Experiments can take the same approach, and although early investigations produced some puzzling results, when experimental techniques with sufficient

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resolution were applied to the problem, a quite reasonable balance of time-averaged measured forces could be demonstrated (Spedding *et al.* 2003).

## 2. ROBINS

In a recent paper (Hedenström *et al.* 2006*b*, hereafter termed HRS06), two robins (*Erithacus rubecula*) flying in a wind tunnel were studied using quantitative flow visualization techniques to analyse the wake disturbances made by the wings and the body. It was only the second species of flying birds for which such measurements had been recorded, and we wished to discover how general were the previous results obtained for a single thrush nightingale (*Luscinia luscinia*), and also what might be the degree of individual variation in the far-field wake within a species.

We found that the robin wakes looked much like the thrush nightingale wakes (figure 1*a*), with patches of wake vorticity that decreased gradually in integrated magnitude as the flight speed increased. Similar calculations as in Spedding *et al.* (2003) showed a similar approximate force balance between the known weight and the measured vertical wake momentum flux. There was no significant difference between the two individuals in any of the measured wake quantities. This was an expected result, because the analysis is not simply based on a statistical compilation of primitive variables, but is predicated on expected relationships in aerodynamic models involving the mass, $m$, the wing span, $b$, and the wing area, $S$. When such a theoretical model is available, it is better to make careful measurements of just one individual rather than attempt to assemble population statistics of less well-trained birds whose variations in flight pattern will only obscure the basic flight mechanics questions. In future, as models and experimental methods become more sophisticated, individual variations may emerge, but on the level of detail of current models, variations in $m$, $b$ and $S$ are sufficient to account for all observations.

The second major result came from a comparison of quantitative wake data from all existing published sources at that time (table 2 in HRS06). At any wing section, one might expect the local circulation $\Gamma$ to scale with the mean flow speed, $U$, and the wing chord, $c$, and an accordingly normalized (dimensionless) circulation, $\Gamma/Uc$, can be predicted to take the form

$$\frac{\Gamma}{Uc} = \frac{W}{S}\,\frac{1}{2q}, \tag{2.1}$$

where $q = 1/2\rho U^2$ is the dynamic pressure. Equation (2.1) follows immediately from the expansion of equation (1.1) to a wing of finite span $b$ whose planform area is $S = bc$ under the condition $L = W$ (and ignoring the further increment in $\Gamma$ required to also balance the drag). Substituting literature values for measured $\Gamma$ for birds of known mass, flight speed and wing size showed that equation (2.1) was a good predictor of all existing data (see figure 2 for an updated version). Despite the fact that the bird wakes themselves appeared rather complex in structure, the strongest circulatory motions

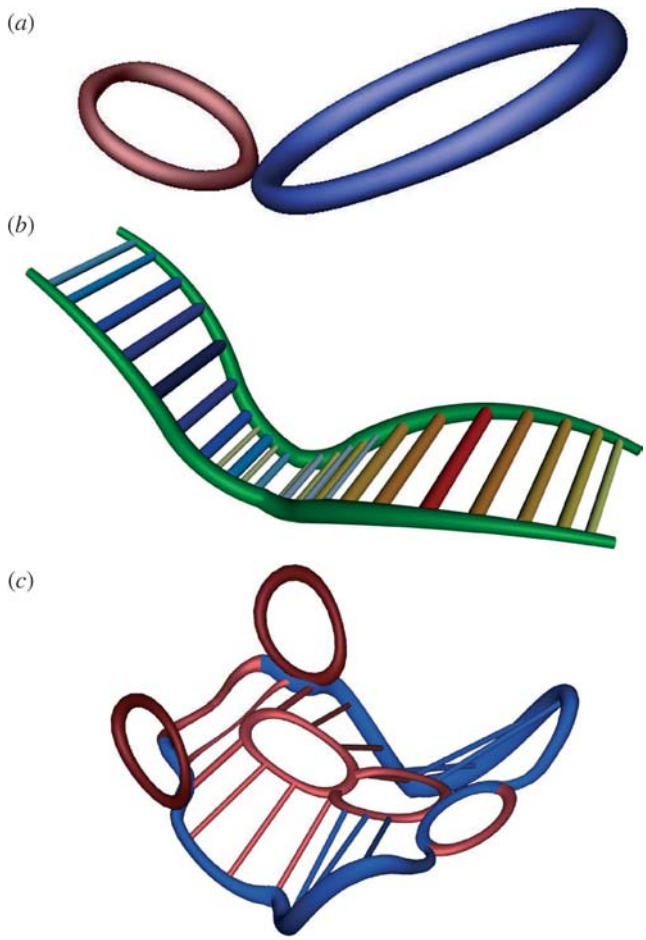


Figure 1. A range of vortex wakes from (*a*) thrush nightingale (Spedding *et al.* 2003), (*b*) swift (Henningsson *et al.* 2008) and (*c*) phyllostomid bat (Hedenström *et al.* 2007). The animals themselves can be imagined to be flying obliquely into the page, from lower right to upper left. By the time these wakes have been measured, the flyers themselves are several wingspans upstream. The tubes show concentrations of vorticity and are colour-coded with red and blue for structures that originate from up- and downstroke, respectively. Green in (*b*) is the inferred trailing vortex shed at the wingtip throughout the wingbeat of the swift. The flight speeds are (*a*) 7 m s$^{-1}$, (*b*) 8.4 m s$^{-1}$ and (*c*) 4 m s$^{-1}$, which is in the mid-range for each species.

in any of them can be predicted from equation (1.1) applied to support the weight of a body in steady horizontal, essentially steady, gliding flight.

Finally, HRS06 noted that, although the wake of any non-accelerating self-propelled body would have exactly zero net momentum flux in the horizontal direction (the thrust exactly balances the drag and both appear as wake motion), if the positive and negative momentum components appear in different forms (many small-scale disturbances versus a small number of larger events) or in different locations (viscous drags along small vortex cores versus the net thrust of the larger-scale wake geometry), then an approximate estimate of the total drag might nevertheless be made from the wake measurements. For the robins, such a calculation yielded an $L/D \approx 7.5$ at $U = 9$ m s$^{-1}$. The significance of this single number is hard to evaluate since it cannot be readily compared with an alternative, but the accurate estimation of the body and wing

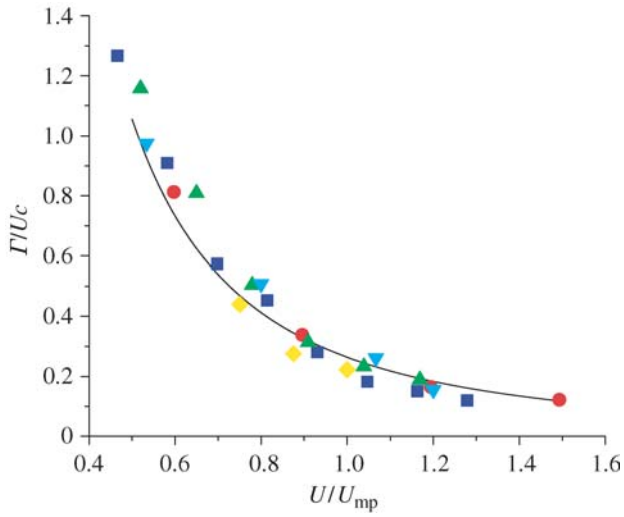


Figure 2. The normalized circulation as a function of flight speed (normalized by some characteristic flight speed, here chosen as $U_{mp}$, the minimum power speed) collapses all the DPIV-based data for far wakes that contain large coherent patches of vorticity. The solid line is equation (2.1). Square, thrush nightingale; circle, house martin; up triangle, robin 1; down triangle, robin 2; diamond, redstart.

drag on birds has long bedevilled the literature and arguments persist over factors of two, so it represented an encouraging start for future improvements.

## 3. BEYOND ROBINS

Since, or contemporaneous with, the appearance of HRS06, exciting new findings have emerged, many of them based on similar digital particle imaging velocimetry (DPIV) methods. Warrick *et al.* (2005) estimated the circulations of patches of vorticity shed on the down- and upstroke of hovering hummingbirds and concluded that hummingbirds generate approximately three-quarters of their lift during the downstroke, contrary to what one might expect from the roughly symmetric wingbeat. Small differences in the angle of attack and the presence or absence of inferred unsteady separated vortices were given as possible reasons for this asymmetry. Although insect wing motions are usually thought to be symmetric with a roughly 50 : 50 contribution on down- and upstroke, computational studies show a balance of 60 : 40 for a hawkmoth model (Liu *et al.* 1998) and even 40 : 60 for a fruitfly (Aono *et al.* 2008). The sensitivity of flight power efficiency to families of wingbeat kinematics has been examined by Wang (2008), who reports multiple close-to-optimal solutions. The reported 40 : 60–60 : 40 spread in relative downstroke contribution to the lift may therefore be unsurprising in both insects and birds.

Further bird species, differing in morphology, kinematics and behaviour, have been studied in the Lund wind tunnel. The house martin (*Delichon urbica*) is an aerial passerine species, hawking insects in the open airspace, with higher aspect ratio wings than those of previously studied passerines. They frequently practise intermittent flight where flapping is interspersed with short gliding intervals, and the wing kinematics showed a curious pause in the upstroke that could be associated with this behaviour. Such a pause during the upstroke has been observed also in the closely related swallow (*Hirundo rustica*) and in house martins studied in another facility (Bruderer *et al.* 2001; Park *et al.* 2001). Although the pause did leave its trace in the wake, the overall pattern and its variation with flight speed were very similar to those of the robins and thrush nightingales studied earlier (Rosén *et al.* 2007). The $\Gamma/Uc$ measure and its predicted dependence on $W$, $S$ and $q$ in equation (2.1) continued to successfully collapse all wake data from all birds at equivalent flight speeds (figure 2). Interpreting $\Gamma/Uc$ as one-half of a local quasi-steady lift coefficient, the similarity suggests that all birds fly at roughly the same mean lift coefficient in cruising flight (approx. 0.4), and further that the higher values of $\Gamma/Uc$ at slow speeds ($U=4\ \mathrm{m\ s^{-1}}$) of a thrush nightingale and robins imply $C_L \approx 2.4$.[1] This is an implausibly high value for steady wings at these Reynolds numbers[2] ($Re_{loc}$ were between 1 and $3\times10^4$ in calculations that included both $U$ and the wing section velocity, which becomes increasingly important as $U$ decreases, for the velocity magnitude on the wing section).

The swift *Apus apus* is well known for its extreme aerial flight style and is thought to land only for nesting. This presents challenges to experimentation, but Henningsson *et al.* (2008) took fledglings whose first ever flight was in the wind tunnel and kept them for long enough for DPIV-based wake signature studies and kinematics measurements before re-release. The swifts have relatively stiff wings, due to a short arm (and humerus) and very elongated primaries, and the wings flex only slightly during the upstroke. The wake signatures for a swift at a typical cruising speed ($U=8.4\ \mathrm{m\ s^{-1}}$) had a different geometry from those of passerines (figure 1*b*). Cross-stream vorticity is continually shed into the wake, tracing the wing path in both down- and upstrokes. During the downstroke, the wing is gradually loaded and then it is gradually unloaded during the subsequent upstroke. The wake has none of the strong coherent structures that hitherto had marked the beginning of the power downstroke in passerines. The quantitative wake analysis and procedures to estimate average force production therefore also had to be modified accordingly. The simple sums of the lift versus weight balanced within experimental uncertainty and an equivalently modified

[1]The lift coefficient, $C_L$, is a (non-dimensional) coefficient that relates the lift, $L$, generated by an aerofoil of planform area $S$ to the dynamic pressure $q\ (=1/2\rho U^2)$, written as $C_L=L/qS$. The maximum probable $C_L$ for an airfoil under steady conditions at these $Re$ is less than 2 (e.g. Laitone 1997).

[2]The Reynolds number ($Re$) is a measure of the relative importance of inertial and viscous forces. An average value can be calculated from the mean wing chord, $c$, the flight speed, $U$, and the kinematic viscosity, $\nu$, as $Re=Uc/\nu$. Local values ($Re_{loc}$) can be defined at specific spanwise locations from a local relative velocity magnitude, $|\boldsymbol{u}_{rel}|$, at the wing section and the chord length there, $c(r)$, where $r$ is the position along the wing. Typical values for small passerines are from 1 to $4\times10^4$ while those for insect wings are rather $10^2$–$10^3$. The aerodynamic performance of wings declines as $Re$ decreases so that smaller flying devices become increasingly reliant on non-conventional force generation mechanisms.

calculation were made to estimate the drag and thrust, given similar caveats as for the robins in HRS06. The swift wake gave an effective $L/D \approx 13$, the highest yet measured from a bird experiment.

Swifts then are different from other birds. Bats turn out to be different again. Bats have evolved powered flight independently from birds, with a membranous wing stretched between elongated finger bones. In slow forward flight, all small passerines (e.g. Spedding *et al.* 2003; HRS06) generate wakes that can be described as single closed-vortex loops. Bats showed two loops, one for each wing (Hedenström *et al.* 2007; figure 1*c*), much as has been reported for some insects (e.g. van den Berg & Ellington 1997*a*; Aono *et al.* 2008). In hovering and slow forward flight, small bats have a distinctive upstroke, where the wing is rotated upside down, developing appropriate camber when loaded (Norberg 1976; Helversen 1986). The quantitative wake signatures confirmed this active upstroke, and also revealed inverted vortex loops shed from the outer wing at the transition between up- and downstroke. Here, the wing tip vortex loop is associated with a negative lift. Overall, the bat wakes appear to be more complex than comparable bird wakes.

For the slow-flying bats, $\Gamma/Uc \approx 2$, and hence the time-averaged lift coefficient of the bat wing would be approximately 4. As $U$ decreases, it becomes a less and less satisfactory measure of the velocity actually experienced by the wing, which is the vector sum of $U$ and the flapping velocity, so this is a crude calculation only, but the $C_L$ thus implied is still a required time average and values greater than half this are already most unlikely. The implication is that something other than what is possible for fixed wings at these equivalent $Re$ must be involved.

A subsequent study of the instantaneous flow field around the bat wing at mid-downstroke (Muijres *et al.* 2008) shows the presence of a large leading-edge vortex (LEV), with sufficient circulation to account for a 40% increase in the lift. This is the first time such a structure has been observed in vertebrate flight, although it is a common object of interest in insect flight, both real (Somps & Luttges 1985; Ellington *et al.* 1996; Willmott *et al.* 1997; Srygley & Thomas 2002; Thomas *et al.* 2004; Bomphrey *et al.* 2005, 2006), and in mechanical model flappers (Maxworthy 1979; van den Berg & Ellington 1997*a*,*b*; Dickinson *et al.* 1999; Birch & Dickinson 2001; Poelma *et al.* 2006) and computer simulations (Liu & Kawachi 1998; Liu *et al.* 1998; Shyy & Liu 2007; Aono *et al.* 2008). It is clear that the LEV dominates the near-wing flow, giving it characteristics that would not be predicted from steady-state analysis or experiments.

Noting that the quantitative similarity of all bird wakes to a simple power glider model encourages a quasi-steady framework, Spedding *et al.* (2008) explored how new results from fixed aerofoils at the same $Re$ could be used to understand the complex animal tracks. One notable inference was that since simple fixed wings of similar aspect ratio and studied at similar chord-based $Re$ have far-field wakes that are as complex and disorganized as those seen in birds and bats (see also Spedding *et al.* 2006), even at a rather low angle of attack, the flow field immediately close to the flapping wing section is likely to be quite well controlled and unseparated at the trailing edge. At the same time, occupying a region in parameter space that is close to abrupt jumps in $L/D$ (as measured in the fixed wings) could be advantageous for control and manoeuvre.

## 4. DISCUSSION

### *4.1. Steady or unsteady?*

'Steady' means time-invariant and 'quasi-steady' has been used to describe situations where time-varying phenomena, such as a flapping wing, can nevertheless be analysed as though the time variation can be accounted for by simply integrating all the various instantaneous configurations (such as variation in $\boldsymbol{u}(r)$, $\alpha$) as they would behave in an equivalent series of time-invariant (steady) flows. 'Unsteady' means that the time history must be taken into account. Fixed wings can produce time-varying forces as separation points move up and down the upper surface, when their induced velocity fields are unsteady. There are other time-varying fluid flows that can only be produced, or understood, given some appropriate time variation of the body geometry itself.

The aerodynamics of simple fixed-wing geometries is already hard to predict, model and understand at the particular range of $Re$ (from 1 to $5\times10^4$) germane to small birds and bats because the onset of laminar separation and its possible reattachment can be very sensitive to small variations in wing geometry or in the ambient environment (velocity, temperature and acoustic disturbances). It is intriguing that the smaller birds and bats occupy this niche, seemingly without random and catastrophic tumbles from the sky. Indeed, if the conditions can be controlled, then being near a parameter domain where small changes can have large physical effects might be desirable, as noted above.

These observations come from results for fixed wings in steady flow. While the fact that quasi-steady values of required circulations seem to be found in all bird wakes encourages the further exploration of quasi-steady models, it is far from proof that the approach is valid, even if it is convenient. On the contrary, the results of Muijres *et al.* (2008) show clearly that the instantaneous flow over a bat wing in mid-downstroke looks nothing like the equivalent steady flow at very slow flight speed ($U \approx 1\ \mathrm{m\,s^{-1}}$), which, at such large angles of attack and with such camber, would be completely separated. It could be that the usual wing properties, including great sensitivity to small variations, are washed away in an entirely new dynamical regime dictated mainly by the properties of the stable large-scale separation at the leading edge.

### *4.2. Far-field wakes and on-wing forces*

The agreement of measured circulations in bird wakes of all kinds with the simple power glider model was at first surprising. How could it be that all wake circulations were the same even though their geometric details were clearly (i) not the same as each other and (ii) all different from a simple, idealized,

rectangular, gliding wake? The answer may be rooted in the fact that all measurements thus far are of far wakes, significantly downstream of the wake generator (the wings) itself. From far off, the main property of any weight-supporting wake is simply the fact that it must have sufficient vertical impulse to support that weight. From far off, this will look like the area traced out by the wingspan times the circulation of the trailing vortices. Small disturbances or fluctuations in the actual span are unimportant in the far field, and just as in inviscid aerodynamic theory the area swept out by a fixed wing is in fact a circle whose diameter is the wingspan, the details of the wing motions and the geometry itself might be expected to be of secondary importance to the basic requirement to support the load of the body. To leading order, this determines the maximum wake circulation, and that is all that can be reliably and repeatedly distinguished in the far wake.

There is much that is not obvious in trying to go from far-wake observations to deductions about forces on the wings themselves. The successful measurement of flow fields over the bat wing confirms this. Other considerations arise too. As we look closer to the fluctuating unsteady velocity fields closer to the wings and the body, we are increasingly obliged to take into account the possible influence of vortex added mass, as summarized clearly in Peng & Dabiri (2008). This term can be thought of as a force that arises when the vortex structures themselves have significant acceleration. The vortices can move parcels of air in front of them much as accelerating solid bodies do. Dabiri *et al.* (2006) have shown how DPIV-generated velocity fields can be analysed to disentangle this force component, but it requires time-resolved data. So far, the late-wake studies of birds and bats do not appear to be strongly influenced by these acceleration terms, as judged by criteria noted in Dabiri *et al.* (2006) and discussed in Hedenström *et al.* (2006*a*, 2007). When time-resolved, near-wake data are available, it will be possible to evaluate this in more detail.

### *4.3. General principles?*

The bat wakes are qualitatively different from standard bird wakes, the house martin wakes have signatures of their characteristic pause in the upstroke and swift wakes are once again quite different from the standard model, albeit in a simplified direction. The above-wing flow shows an attached LEV in bat flight and there is a real possibility that, as the measurement techniques improve in the spatial and temporal resolution, we will be faced with an almost endless supply of intriguingly different wakes, which will look more and more dissimilar as more and more detail is available. (For some time, studies of insect wakes have indicated that a wide variety of patterns can be identified (Brodsky 1991; Grodnitsky & Morozov 1993), and vortex loops and interconnections of extraordinary complexity can be traced, with sufficient care, from even rather simple mechanical flapping or linearly accelerating models (Freymuth 1985; Freymuth *et al.* 1987; von Ellenrieder *et al.* 2003).) If so, this is not necessarily useful progress. The most urgent task is to gain an understanding of *generalizable* principles in animal flight. Because they are general, they can then be extrapolated to new conditions and incorporated into predictive, quantitative models. These can then be applied to the ecology of bird migration or to the design of a small-scale ornithopter for surveillance, for example. Finding the needed common principles might yet prove challenging.

## 5. OUTLOOK

Progress and continued efforts can be predicted along almost all the lines discussed here.

— We will continue to make accurate measurements of forces and instantaneous flow fields on fixed wings because, even if they do not prove of universal interest to flapping animal wings (and not all animal wings flap all the time), there is still a need for reliable quantitative data for human-engineered fixed-wing designs.
— More efforts will go into resolving flows close to the wings and the body of flying animals (noting that experiments must be performed with care and precautions to avoid damaging the eyesight of the subjects when they are close to the bright laser light), following the far- to near-wake progression of the bat experiments. In turn, mechanical models will become more realistic, incorporating more degrees of freedom and passive and active compliance and flexibility.
— Certain advances can be predicted to follow from foreseeable improvements in technology. Thus, it is clear that obtaining time-resolved, three-dimensional velocity fields is not far off (pending the further development of high-repetition-rate lasers), and this will be immensely useful in making more sophisticated calculations of the fluid dynamical forces. Meanwhile, computational fluid dynamic calculations using faster, larger and cheaper computers will attain higher resolution and Reynolds numbers will begin to overlap with those actually used by birds and bats, so that these most difficult regimes that include transition of laminar boundary layers and free shear layers to turbulence can be simulated.
— In the near future, the slightly less glamorous job of calculating the drag on the wings and the body of a gliding animal from fully time-resolved, three-dimensional data in Trefftz planes downstream of the animal will help to resolve the significant (factors of two or more) uncertainties in estimating drag coefficients for real birds, whether still or moving.

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