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The Aerodynamics of Hummingbird Flight

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[Abstract] Hummingbirds fly with their wings almost fully extended during their entire wingbeat. This pattern, associated with having proportionally short humeral bones, long distal wing elements, and assumed to be an adaptation for extended hovering flight, has led to predictions that the aerodynamic mechanisms exploited by hummingbirds during hovering should be similar to those observed in insects. To test these predictions, we flew rufous hummingbirds (*Selasphorus rufus*, 3.3 g, $n = 6$) in a variable-speed wind tunnel ($0\text{--}12\text{ m s}^{-1}$) and measured wake structure and dynamics using digital particle image velocimetry (DPIV). Unlike hovering insects, hummingbirds produced 75% of their weight support during downstroke and only 25% during upstroke, an asymmetry due to the inversion of their cambered wings during upstroke. Further, we have found no evidence of sustained, attached leading edge vorticity (LEV) during up or downstroke, as has been seen in similarly-sized insects - although a transient LEV is produced during the rapid change in angle of attack at the end of the downstroke. Finally, although an extended-wing upstroke during forward flight has long been thought to produce lift and negative thrust, we found circulation during downstroke alone to be sufficient to support body weight, and that some positive thrust was produced during upstroke, as evidenced by a vortex pair shed into the wake of all upstrokes at speeds of $4\text{--}12\text{ m s}^{-1}$.

I. Introduction

WITH a few exceptional intersections, the evolution of human-engineered flight and the study of the evolution of animal flight have been essentially parallel. Given the results of the earliest such meetings (e.g., DaVinci's ornithopter), this has probably been for the best; the disparity in scale between these lineages and its effects on structural and fluid mechanics has necessarily cloistered these two fields and prevented further fruitless and dangerous intercourse. However, interest in the development of micro-air-vehicles (MAVs) has thrown a debutante ball, and it would seem that the convergence, the meeting and mixing of these lines – now working at similar scales and Reynolds numbers (Re) – could produce useful offspring. The key to the viability of such products will be determining which of those characteristics described for biological fliers are results of natural selection, rather than results of ancestry. That is, the utility of our understanding of biological flight to the engineering community rests upon our ability to determine adaptation – a question fundamental to biologists.

Certainly, some of the loveliest of biological models to walk onto the dance floor are the hummingbirds. Possessing the right range of sizes (from 2-20 grams), unmatched aerial performance for animals of those sizes, along with important research intangibles (i.e., tractability and warmth), hummingbirds seem likely sources of useful design

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seeds – places for engineers to start. The purpose of this paper is to describe what is currently known of the biomechanics and aerodynamics of hummingbirds, placed in an evolutionary context that will allow those who might use these animals as models to assess those mechanisms as worthy of emulation.

II. Hovering Flight: Lessons from Convergence?

Thirty-three years after the first rigorous treatment of hummingbird flight by Stolpe and Zimmer in 1939¹, describing the kinematics of hovering, Weis-Fogh (1972)² developed an aerodynamic model of hummingbird flight, noting its similarities to insect flight. Although the fruit flies operated at Re considerably lower than those of the hummingbirds, their kinematic similarities led to the assumption^{2,3,4}, that the aerodynamic mechanisms were also similar – most notably in that the two halves of the wingbeat cycle were roughly similar in aerodynamic force production. More recently, flow visualization and dynamically-scaled robotic simulations of insect flight^{5,6} demonstrated that the half-strokes of insects similar in size to hummingbirds, were indeed aerodynamically active and equal, and that lift was generated through leading-edge vorticity (LEV) attached to the dorsal surface of the translating wing. Hummingbird wings, modeled as flat plates and flown in a dynamically-scaled robot, produced similar LEVs and symmetrical force when flown at kinematic angles of attack observed in hovering hummingbirds (Fig.1). The inferences it made to hummingbird flight were clear and compelling; the demonstration of convergence, from two such long-diverged evolutionary lines, on the same locomotor mechanism would make a profound statement to MAV engineers: there's only one way to hover a small, flapping vehicle.

We tested the assumptions of half-stroke symmetry using 2-D digital particle image velocimetry (DPIV), sampling the wake of hummingbirds in both the frontal and parasagittal plane (see Appendix) allowing us to capture tip and starting/ending vorticity respectively. We found that hummingbirds exhibit marked asymmetry in lift force production, with 75% of the body weight lift support being generated during the downstroke – in essence, about half-way from the typical bird condition (100% of lift during the downstroke) and the typical insect⁷ (Fig.2). Given the respective wing speeds and areas of the two half-strokes, we concluded that this asymmetry was at least in part due to the positive camber of the hummingbird wing, which does not completely reverse during upstroke. However, the far-field wake, remarkably similar to that produced by hawkmoths⁶ (Fig. 3) did suggest that LEVs were present during at least the downstroke, and that hummingbirds might be true hovering chimeras. While it seemed certain that leading-edge vorticity was formed at some point during the downstroke, the question of the intent and purpose of such flow remained.

Preliminary examination of the near-field flow around hummingbird wings during both half-strokes reveals that no attached, stable leading-edge vorticity is developed during the

Figure 1. DPIV vector field. Flow around a dynamically-scaled robotic simulation of hummingbird wings. Wings were modeled as flat plates; angle of incidence = 15° . Note clockwise attached LEV above wing.

Figure 2. Frontal plane vorticity ($Rot Z [dx/dy]$) field of a hovering hummingbird. Upper vortex pair (a) are tip vortices from upstroke; lower pair were produced by the previous downstroke.

Figure 3. Parasagittal plane vorticity. ($Rot Z [dx/dy]$) field of a hovering hummingbird. Upper vortex (a) is the starting vortex of upstroke; (b) putative LEV, produced by the rapid pitch up of the wing; (c) ending vortex of downstroke.

majority of the wing translation (Fig. 4); that is, the flow is essentially laminar, and typical lifting line aerodynamics probably explain the majority of lift production. The vorticity seen in the far-field wake would seem to be a result of a transient LEV produced by the rapidly-pitching airfoil at the end of the downstroke – an effect typical of a dynamically-stalling airfoil. However, the flow at the leading edge of the wing is not entirely typical; in particular, the stagnation point of the airflow is deep – several millimeters back from the leading edge on the ventral side of the wing. The movement of air from this ventral point, around the leading edge to the dorsal surface of the wing ostensibly creates a vortex with a center at the anatomical leading edge of the wing. In outward appearance, this flow is similar to that around the leading edge of fixed (i.e, gliding) swift wings⁸, but due to the differences in wing presentation (strongly swept in the swift versus straight in the hummingbird) the equivalence of these structures cannot be determined.

The observed difference in flow between the robotic model and real hummingbird wing (Figs. 1, 4) may have several origins; the two most immediately recognizable are both a result of the effects of camber. As previously suggested, the greater lift coefficients generated by cambered wing of the real bird generated greater downwash during downstroke, forming the basis of half-stroke disparity. This greater downwash also lowers the effective angle of attack; the 25°-30° angle of incidence in early downstroke is reduced to 9°-15° when a near-field downwash of 3 ms⁻¹ is incorporated into the calculation of angle of incidence. The flow around a flat plate at this angle may be more similar to the observed flow around hummingbird wings.

The aerodynamic properties of feathers cannot be discounted as a source of the unique flow around hummingbird wings, and studies of the effects of the microstructure of feathers on boundary-layer interactions – either through surface ‘tripping’ or airfoil transmissivity, are probably warranted.

Figure 4. Flow around a hummingbird wing. DPIV vector field of flow around a hummingbird mid-wing at mid-downstroke. Red line indicates the position of the chord x-section, moving left to right. Note the absence of dynamic stall vorticity, present in the robotic simulation (Fig. 1), above the wing.

III. Forward flight

While the advantages of leaving the wing extended during the upstroke during hovering are clear, there are good theoretical reasons^{4,9}, and some experimental evidence^{10,11} to suggest it may be a liability at low forward flight speeds and during acceleration. During upstroke, the supinated wing should produce a lift force with a rearward vector component, producing negative thrust, adding to the profile drag already produced by the wing. Thus, most small birds flex their wings during the upstroke, completely ceasing lift production and avoiding these aerodynamic penalties¹² – which, for small birds, with relatively low inertia, may be severe. Perhaps owing to the anatomical commitment to hovering flight, hummingbirds leave their wings extended during upstroke at all flight speeds. The far-field wake of hummingbirds indicates that lift production indeed continues

Figure 5. Wake of a hummingbird. Forward flight, (6 ms⁻¹). Note the downstroke starting (a) and ending vortices (b), and the vortex pair, hypothetically a result of a secondary ‘post-ending’ vortex at mid-upstroke (c) and a ‘pre-starting’ vortex (d) produced in quick succession. The interaction of this vortex pair suggests thrust production.

throughout the upstroke; however, there is little to suggest that negative thrust is produced during this type of upstroke. Indeed, the shedding of a vortex pair at mid-to-late upstroke, coinciding with the point in the upstroke where the speed of the upward translation of the wing has reduced angle of incidence to zero (Fig. 5), suggests that some thrust may be generated during this portion of the wingbeat cycle. The strength and utility – and ubiquity among other birds with aerodynamically active upstrokes – of this mechanism to hummingbirds have yet to be determined, but it is probably insufficient to overcome the aerodynamic costs of active upstrokes in birds (or MAVs) with larger wings. Evidence from the anatomy and performance of swifts¹⁰ suggests that unusually large pectoral muscles (and, hence, particularly strong downstrokes for thrust production) are required to overcome the costs incurred by stiff wings and active upstrokes.

IV. Conclusion

DPIV analysis of live birds and robotic simulations suggests that for thin wings at low Re , cambered airfoils generate greater lift coefficients than flat plates (or other such symmetrical sections), and it seems likely that the asymmetry in the half-strokes of hovering hummingbirds is clearly an artifact of its avian ancestry – ancestors for which the downstroke (or just a wing extended in glide) was the only lift generating portion of the wingbeat cycle. Given that symmetry in lift production offers some advantages (e.g., more continuous availability of lift force for needs of maneuvering; smaller vertical oscillations in body movement between the half-strokes), there would be little use in incorporating this particular aspect of hummingbird flight into a MAV. However, emulating the rigid and kinematically simple wing of hummingbirds may be extremely useful, given its performance over a range of speeds.

Appendix

A. Circulation and Weight Support

To compute vorticity (ω , s^{-1}), we post-processed vector fields using a median filter, and then computed $\text{rot } z[dy/dx]$. We measured circulation (Γ , $m^2 s^{-1}$) in the trailing tip vortices by integrating ω with respect to area (m^2). We limited our analysis to views where vortex cores were normal to the sampling plane (parasagittal: centered at midwing; frontal: centered at wing root). We tested whether observed Γ was sufficient to support body weight by comparing Γ with circulation required ($\Gamma_o) = WT / \rho S$ where W is body weight (N), T is time per wingbeat (s), and S is the projected horizontal area swept by the two wings (m^2)¹³.

B. Kinematics

Separate flight trials ($n = 4$ birds) were recorded using two synchronized high speed digital video cameras operating at 500 Hz sampling and shutter speed of $1/1000$ s. We merged two-dimensional coordinates from each camera into a single 3-d coordinate space using the direct linear transformation (DLT) coefficients derived from a 16-point calibration frame¹⁴. Using these data, we calculated angular velocity of the wing ($rad s^{-1}$) and angle of attack of the mid-wing (degrees) relative to incurrent air flow. Incurrent air velocity was the sum of translational

Figure 6. Position of Hummingbirds hovering. DPIV laser light sheet illustrating the frontal (a,b) and parasagittal (c,d) sampling planes and revealed wake structures.

velocity of the wing and average 3-d air velocity computed using DPIV data from frontal and sagittal planes, which is dominated by a mean downward velocity of 1.1 ms^{-1} .

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