Leading edge vortex in a slow-flying passerine

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Most hovering animals, such as insects and hummingbirds, enhance lift by producing leading edge vortices (LEVs) and by using both the downstroke and upstroke for lift production. By contrast, most hovering passerine birds primarily use the downstroke to generate lift. To compensate for the nearly inactive upstroke, weight support during the downstroke needs to be relatively higher in passerines when compared with, e.g. hummingbirds. Here we show, by capturing the airflow around the wing of a freely flying pied flycatcher, that passerines may use LEVs during the downstroke to increase lift. The LEV contributes up to 49 per cent to weight support, which is three times higher than in hummingbirds, suggesting that avian hoverers compensate for the nearly inactive upstroke by generating stronger LEVs. Contrary to other animals, the LEV strength in the flycatcher is lowest near the wing tip, instead of highest. This is correlated with a spanwise reduction of the wing’s angle-of-attack, partly owing to upward bending of primary feathers. We suggest that this helps to delay bursting and shedding of the particularly strong LEV in passerines.

Keywords: leading edge vortex; aerodynamics; aeroelastics; bird flight; pied flycatcher; wind tunnel

1. INTRODUCTION

Most insects and hummingbirds use horizontal stroke-plane hovering, where weight-supporting lift forces are generated during both the downstroke and upstroke [1,2]. Unlike hummingbirds, most conventional birds use inclined stroke-plane hovering where the majority of the flight forces are produced during the downstroke and upstroke [1,3,4]. During the upstroke, the wing is retracted and the primary feathers are spread and held at a low angle-of-attack, resulting in small vertical forces [4–6]. To compensate for the low weight support during the upstroke, lift forces during the downstroke need to be relatively higher in inclined stroke-plane hovering when compared with horizontal stroke-plane hovering, and thus the use of some lift-enhancing aerodynamic mechanism may be expected [4,5].

Within all major extant flying taxa (insects, bats and birds) animals have been found to use leading edge vortices (LEVs) to enhance lift [7–9], making the LEV arguably the most important and widely used lift-enhancing aerodynamic mechanism in natural flyers. Although LEVs have been found in a swift model [10] and a goose flapper [11] in cruising flight, LEVs have primarily been studied in slow and hovering flight [7–9]. In this case, the wing typically operates at high angles-of-attack (greater than 20°), which causes the airflow to separate at the wing’s leading edge [12]. If the flow re-attaches to the wing before the trailing edge, either an LEV or separation bubble is generated [13]. For flapping wings with sufficiently low reduced wavelength (λ < 4–5), Reynolds numbers (Re = 10^2–10^3) and Rossby number (Ro < 3), the LEV or separation bubble will not burst but remain attached to the wing until the end of the downstroke [13–15].

Here, we study the flow dynamics around the wing of an inclined stroke-plane hoverer, the pied flycatcher (Ficedula hypoleuca), flying freely in a wind tunnel at a flight speed of U∞ = 1 m s⁻¹, to investigate how the pied flycatcher is able to generate enough lift at low flight speeds [4]. The flycatcher is a small (14 g) insectivorous passerine that mainly hunts insects on the wing while hovering and flying slowly.

2. MATERIAL AND METHODS

Two juvenile pied flycatchers (electronic supplementary material, table S1) were trained to fly in a wind tunnel at U∞ = 1 m s⁻¹. The airflow around the birds was measured using particle image velocimetry in two planes (electronic supplementary material, figure S1) [5,6]. Using a vertical transverse plane (x–z) close behind the animal, we measured tip-vortex dynamics throughout the downstroke following Muijres et al. [5], for both individuals (28 wingbeats). Using an on-wing set-up with vertical streamwise plane (x–z), we measure the airflow dynamics near the wing surface and the corresponding wing kinematics following Muijres et al. [8], for flycatchers. For on-wing measurements where an attached vortex structure (AVS) was present on top of the wing, and its view was not blocked by the wing, we estimated the AVS circulation following Muijres et al. [8]. During the on-wing sessions the bird was wearing goggles for eye protection (figure 1). Each measurement was given a normalized time-stamp t = t/T, where t is time and T is wingbeat period; τ = 0 and τ = T are the start and end of the downstroke, respectively (T is the temporal downstroke ratio). The on-wing measurements were also given one of four spanwise locations (electronic supplementary material, figure S2): two arm wing sections (‘inner wing’ and ‘mid wing’) and two hand wing sections (‘outer wing’ and ‘wing tip’).

From the wing kinematics data we determined the downstroke average effective angle-of-attack αeff and the downstroke average effective wing speed Ueff = U(t)/v, following Muijres et al. [9] (t is the normal time and v is the kinematic viscosity of air, and ̅ is average chord-length [12]; downstroke-based Strouhal number Str = fUeff/c, following Muijres et al. [8], for each wing section separately as well as for the complete wingspan (and ̅ are the horizontal and vertical wing downstroke flapping velocities, respectively). Downstroke average velocities were estimated as the average of sine functions fitted through the U(t) distributions (MATLAB, fit), while αeff is the average of all αeff(t) measurements. Additionally, we determined—at each wing section and for the complete wing—the downstroke average effective Reynolds number Reeff = Ueffc/ν, where v is the kinematic viscosity of air, and ̅c is average chord-length [12]; downstroke-based Strouhal number Str = fUeff/c, following Muijres et al. [8], for each wing section separately as well as for the complete wingspan ( and ̅c are the horizontal and vertical wing downstroke flapping velocities, respectively). Downstroke average velocities were estimated as the average of sine functions fitted through the U(t) distributions (MATLAB, fit), while αeff is the average of all αeff(t) measurements. Additionally, we determined—at each wing section and for the complete wing—the downstroke average effective Reynolds number Reeff = Ueffc/ν, where v is the kinematic viscosity of air, and ̅c is average chord-length [12]; downstroke-based Strouhal number Str = fUeff/c, following Muijres et al. [8], for each wing section separately as well as for the complete wingspan ( and ̅c are the horizontal and vertical wing downstroke flapping velocities, respectively). Downstroke average velocities were estimated as the average of sine functions fitted through the U(t) distributions (MATLAB, fit), while αeff is the average of all αeff(t) measurements. Additionally, we determined—at each wing section and for the complete wing—the downstroke average effective Reynolds number Reeff = Ueffc/ν, where v is the kinematic viscosity of air, and ̅c is average chord-length [12]; downstroke-based Strouhal number Str = fUeff/c, following Muijres et al. [8], for each wing section separately as well as for the complete wingspan ( and ̅c are the horizontal and vertical wing downstroke flapping velocities, respectively). Downstroke average velocities were estimated as the average of sine functions fitted through the U(t) distributions (MATLAB, fit), while αeff is the average of all αeff(t) measurements. Additionally, these data were normalized using the wingspan average Ueff and ̅c (1 = f/T Ueffc), which enabled us to compare local circulation estimates directly. The average normalized temporal tip-vortex circulation distribution f/τ was determined by fitting a smoothing spline (MATLAB, csaps smoothing parameter = 1–10⁻⁷), following Muijres et al. [5], for each wing section, the temporal variation in circulation of any AVS (f/τ(t)) was estimated using a linear least squares fit (MATLAB, polyfit) for 0 < r < 0.25. The downstroke average lift-coefficient was defined as Cl = f/τtip [5], where the contribution to Cl by the presence of an AVS is CANS = 2f/τtip [8] (1 = f/T is downstroke average 1). The lift-to-weight ratio is C(w) = mReffUeffc/2fUeff ≡ Mg [5], where...
\( \rho \) is air density, \( b_{\text{eff}} \) is the downstroke average effective wingspan estimated from the tip-vortex span (MATLAB, csaps smoothing parameter \( \lambda = 1 - 10^{-2} \)), and \( M_g \) is weight.

3. RESULTS

At \( U_\infty = 1 \text{ m s}^{-1} \), wingbeat frequency was \( f = 13.9 \text{ Hz} \) and \( R_{\text{fl}} = 0.50 \); see figure 2c,d and electronic supplementary material, table S2 for additional results on kinematics.

The vorticity field above the flycatcher wing shows that the flow separates at the leading edge, resulting in a patch of high vorticity called the AVS (figure 1). The AVS is present at all the measured spanwise locations, but it is stronger at the arm wing (figure 1a,b) than at the hand wing section (figure 1c,d). The induced velocity field between the wing surface and the AVS shows reversed flow (figure 1a,c), and instantaneous streamlines, based on the velocity field, show the presence of a recirculation region within the AVS (figure 1b,d).

For all wing sections, \( C_{\text{AVS}}^{\tau}(\tau) \) increases with \( \tau \) from the start of the downstroke until at least mid downstroke (0 \( < \tau < 0.25 \), figure 2a). This increase is stronger at the arm wing section than at the hand wing (figure 2a), resulting in the highest average \( C_{\text{AVS}}^{\tau} \) at the arm wing section (figure 2b). Based on \( C_{\text{tip}} = 1.32 \) and \( b_{\text{eff}} = 0.88 b \) (\( b \) is maximum wing span, electronic supplementary material, table S1), we estimated \( L/W = 0.99 \) and \( C_{\text{L}} = 2.76 \). Comparing \( C_{\text{AVS}}^{\tau} \) with \( C_{\text{tip}} \) shows that the AVS contributes on average 49 per cent to the lift production.

4. DISCUSSION

The wake-estimated \( C_{\text{L}} = 2.76 \) results in 99 per cent weight support and suggests the use of a lift-enhancing mechanism [17]. This \( C_{\text{L}} \) estimate is about half that estimated based on a kinematic analysis of a hovering flycatcher [4]. The difference is most likely explained by differences in the analysis method (wing average versus a blade element analysis), and the fact that the inner wing section generates significantly more lift at \( U_\infty = 1 \text{ m s}^{-1} \) compared with hovering, resulting in a lower required \( C_{\text{L}} \).

Throughout the downstroke, no large-scale vortex shedding associated with separation was observed in the wake of the flycatcher wing, and therefore the AVS could refer to either a separation bubble or an attached LEV [13]. A separation bubble typically occurs at relatively low angles-of-attack (\( \alpha \approx 7^\circ \)), where laminar airflow separates from the wing surface and re-attaches to the wing after it has become turbulent. The resulting separation bubble has a relatively small height, and—with increasing angle-of-attack—it grows primarily in the chordwise direction towards the trailing edge [12,18]. LEVs, on the other hand, are typically produced by wings at relatively high angles-of-attack (\( \alpha > 20^\circ \)), separation typically occurs at the leading edge, and LEV height is similar to its chordwise width [7–9,13,19]. As the flycatcher wing operates at a relatively high angle-of-attack during the downstroke (figure 2d), the AVS is located at the leading edge and it is almost circular in shape (figure 1), we think the observed AVS should be...
labelled a LEV. This is further supported by the continuous increase of $G_{AVS}(t)$ throughout the downstroke (figure 2a), suggesting the LEV might be unstable [13,14]. Thus, from hereon we will refer to the AVS as a LEV.

The 49 per cent LEV lift contribution in flycatchers is lower than the 65 per cent found in a model hawkmoth [20], similar to the 42 per cent in similar sized bats [8] and the 45 per cent in a model fruitfly [21], but higher than the 16 per cent in hummingbirds [9]. The difference in LEV strength in the flycatcher when compared with that in hummingbirds could be owing to the difference in upstroke function. The hummingbird generates 25 per cent of its total lift during the upstroke [2], while the flycatcher produces almost no weight support during the upstroke (electronic supplementary material, figure S3) [4–6]. To compensate for a low weight supporting upstroke, the flycatcher needs to generate relatively more lift during the downstroke, which might be achieved by producing a relatively strong LEV.

For the flycatcher, $G_{AVS}$ was highest at the arm wing section and lowest near the wingtip (figure 2b), electronic supplementary material, figure S2). This is different from the spanwise LEV distribution observed in all previously studied animals, figure S3b) [4–6]. To compensate for a low weight supporting upstroke, the flycatcher needs to generate relatively more lift during the downstroke, which might be achieved by producing a relatively strong LEV.

The experiments were carried out in accordance with university guidelines and approved by the university ethical committee for research involving animals.

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