The flapping flight of birds
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Document Version
Publisher's PDF, also known as Version of record

Publication date:
2014

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):

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Chapter III

The Influence of Wing Morphology on the 3D Flow Pattern of a Flapping Wing at Bird Scale
Chapter III

Submitted to the Journal of Fluid Mechanics

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*The influence of wing morphology on the 3D flow pattern of a flapping wing at bird scale*
The influence of wing morphology

ABSTRACT

The effect of airfoil design parameters, such as airfoil thickness and camber are well understood in steady-state aerodynamics. But this knowledge cannot be readily applied to the flapping flight in insects and birds: Flow visualizations and computational analyses of flapping flight have identified several unsteady effects that contribute substantially to the generation of aerodynamic force. In flapping flight, high angles of attack and partly separated flow are common features. Therefore, it is expected that airfoil design parameters affect unsteady wing aerodynamics differently. Existing studies focussed on force measurements, which don’t provide sufficient insight into the dominant flow features.

To analyze the influence of wing morphology in slow-speed bird flight, the time-resolved, three-dimensional flow field around different flapping wing models in translational motion at a Reynolds number of $22,000 < Re < 26,000$ was studied. The effect of several Strouhal numbers ($0.2 < St < 0.4$), camber and thickness on the flow morphology and on the circulation was analyzed.

A strong leading-edge vortex was found on all wing types at high $St$. The vortex is stronger on thin wings and enhances the total circulation. Airfoil camber decreases the strength of the leading-edge vortex, but increases the total bound circulation at the same time, due to an increase of the ‘conventional’ bound circulation of the wing. The measurements show that wing design in the slow-speed flight of birds is important and affects the ratio of ‘conventional’ bound circulation and the additional circulation enabled by leading-edge vortices.
INTRODUCTION

The wing morphology parameters thickness and camber have received much attention ever since the first aircraft were designed (e.g. Lilienthal, 1889). Therefore, a substantial knowledge about the influence of wing morphology under steady flow conditions exists. Wing camber increases lift and the maximal lift-to-drag ratio (L/D) for wings operating both at low and at high Reynolds numbers (Re, Shyy et al., 2008). The aerodynamic effect of wing thickness and leading-edge radius, however, strongly depends on Re. High Re are mostly relevant for manned aviation. Here, a relatively thick wing is advantageous, since the range of acceptable angles of attack (α) becomes wider, and flow separation due to an unfavourable chordwise pressure gradient on the wing occurs much later than on a thin wing (Shyy et al., 2008). In contrast, low Re flyers like insects, birds and bats require thin wings to operate efficiently. At low Re, thin wings create more lift (Kunz, 2003) and less drag (Okamoto et al., 1996), which leads to a better L/D and increases performance.

As recent studies have shown, the aerodynamic situation during bird flight deviates from the steady flow conditions that are generally assumed for airplane wings. Unsteady effects during flapping flight are more important than thought so far. Lift-enhancing flow features have been found on the flapping wings of a hovering hummingbird (Warrick et al., 2005), a robotic goose (Hubel & Tropea, 2010), and during the slow-speed flight of a passerine (Muijres et al., 2012c; Chang et al., 2013).

The aerodynamic mechanisms that increase forces in the slow-speed flapping flight of birds might be similar to the mechanisms studied in detail in insect flight: Insects generate aerodynamic forces by flapping their wings with high aerodynamic angles of attack (Ellington, 1984b). Several aerodynamic effects, such as clap-and-fling, rotational lift and wake capture, increase the forces generated by the wings. The most prominent flow feature found in insect and bird flight is the leading-edge vortex (LEV, e.g. Ellington et al., 1996). A LEV is a region of recirculating fluid which is closely attached to the top of the wing; it increases the total bound circulation and the force coefficients. This vortex is largely responsible for the increased performance of flapping wings at relatively low Re (e.g. Bomphrey et al., 2005). In contrast, in a purely two-dimensional flow, a leading-edge vortex would grow quickly and detach from the wing, initiating large scale van Kármán-like vortex shedding, hence a full detachment of the flow (e.g. Dickinson & Gotz, 1993). But in the three-dimensional context of flapping wings, a spanwise pressure gradient is assumed to transport vorticity away from the LEV towards the wing tip, inhibiting excessive vortex growth and vortex shedding (e.g. Ellington et al., 1996; Usherwood & Ellington, 2002a). Additionally, vortex stability is increased by the relatively short duration of a down- respectively upstroke: Large effective angles of attack occur only for a limited time which reduces the amount of vorticity accumulation and therefore the
size of the vortex (Wang et al., 2004; Bomphrey et al., 2005). Due to the partly detached nature of this robust high-lift flow system, it is uncertain, whether the knowledge about wing morphology under steady flow conditions is also valid for flapping wings.

Some research on the influence of wing camber, wing thickness and leading-edge radius in wings with unsteady motion has already been completed. Dickinson & Gotz (1993) performed force measurements of a wing that accelerates rapidly from rest at very low Re (80 < Re < 200). Cambering of the airfoil did not increase the performance of the wing. Later studies used revolving wings to analyse the influence of wing morphology. These studies mimicked hovering flight and concentrated on force measurements at 5,000 < Re < 10,000. At Re = 8,000, wing camber and leading-edge detail did not noticeably influence the forces created by revolving wings (Usherwood & Ellington, 2002a). At very similar Re, but in a different study, wing models with sharp leading-edges or wing camber were shown to have higher lift coefficients than wings without these features (Altshuler et al., 2004). Hence, the influence of wing morphology with flapping wings at low Re seems to be inconclusive, and not strictly in agreement with the findings from steady flow experiments. However, these studies focussed on the net output forces created by the wings and did not consider the flow morphology. Additionally, experiments with flapping and translating wings at higher Re, which are more relevant for the slow-speed flapping flight of birds, were not yet carried out.

The present study focusses on the four-dimensional (three-dimensional + time) flow pattern for a range of flapping frequencies. The flow around several flapping wing models is visualized using digital particle image velocimetry (DPIV) in water. One of the goals of the study is to test the validity of the results from low Re insect flight for the slow speed flapping flight of birds at higher Re. The study will also illustrate the potential role of spanwise flow for LEV stabilization. The influence of airfoil camber and thickness on the flow patterns and the consequences for the bound spanwise circulation (defined as the circulation around the spanwise axis) will be analyzed.
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MATERIAL AND METHODS

In practice, the flow around flapping and translating wing models will be visualized in water at appropriate Reynolds number and flapping frequency. By combining series of two-dimensional velocity information gathered with (DPIV), a full three-dimensional representation of the flow is created. These data allow investigating the time-resolved 3D flow patterns and consequent forces respectively circulation and the influence of wing morphology.

WING MODELLING

The wing models are based on airfoil data of a pigeon (*Columba livia domestica*). Bachmann (2010) provides information on the planform of the wing and on the maximum thickness of the airfoil, and Biesel et al. (1985) measured the position of maximum thickness, maximum camber and the position of maximum camber on a freely gliding pigeon. The reported airfoil parameters from 10 to 60% of wingspan were averaged and applied to the airfoil at the wing root. The airfoil thickness was subsequently linearly reduced towards the wingtip, as indicated by the airfoil data of real birds. The parameters were used to generate airfoil coordinates (NACA 4-digit, modified series) for a 3D model wing. The planform of the model wing, including the aspect ratio and the chord distribution over span, was simplified from the data given in Bachmann (2010). The wings were designed in Rhinoceros 3.0 (Robert McNeel & Associates, Seattle, USA). A 3D printer (ZPrinter™ Z310, layer thickness 0.1 mm, resolution 300 x 450 dpi, Z Corporation, Burlington, USA) was used to create positive moulds that were casted with silicone (ELASTOSIL® M 4630, Wacker Chemie AG, München, Germany). The final wing models were created using transparent epoxy (Epoxy casting resin waterclear, Poxy-Systems® by R&G, Waldenbuch, Germany, density 1.09 g/cm³, refractive index 1.53).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Wing base</th>
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<th>Wing tip</th>
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<tr>
<td>Chord [mm]</td>
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<tr>
<td>Max. thickness [% of chord]</td>
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<tr>
<td>Max. thickness position [% of chord]</td>
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<tr>
<td>Max. camber [% of chord]</td>
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<td>5</td>
<td>5</td>
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<tr>
<td>Max. camber position [% of chord]</td>
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<td>37</td>
<td>37</td>
</tr>
<tr>
<td>Nose radius [1] (1 = same as original airfoil, 0 = sharp)</td>
<td>1</td>
<td>0.5</td>
<td>0.1</td>
</tr>
</tbody>
</table>

Tab. 3.1: Geometry of the standard model wing.
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Fig. 3.1: Wing model (type ‘s’). Wing length = 120 mm, position of spanwise joint = 30% of chord length. The mean chord length of the wing is 43.75 mm.

Fig. 3.2: The five wing models that were tested. From left to right: Low camber, high camber, standard, low thickness, high thickness.

In addition to the standard model wing (type ‘s’, see Table 3.1), which was based on a pigeon wing (see Figure 3.1), four other wing models were tested in the current study (see Figure 3.2). In each wing model, a single airfoil parameter was altered: Wing ‘c+’ (high camber) is identical to type ‘s’, except for the camber, which was increased by a factor of two for all wing sections. Wing ‘c-’ (low camber) has the same base-airfoil with zero camber. In wing ‘t+’ (high thickness) the maximum thickness was increased to 15%, and in wing ‘t-’ (low thickness), the thickness was decreased as much as technically possible (3%).

FLOW TANK AND KINEMATICS

All measurements were performed in a flow tank. For the same Reynolds and Strouhal number, the flow velocity as well as the flapping frequencies can be reduced, which sim-
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**Fig. 3.3:** Definition of the geometric angle of attack ($\alpha_{geo}$) and the excursion angle ($\Phi$). The geometric angle of attack is defined as the angle between the free flow and the wing chord. The excursion angle is the angle between the horizontal and the wing.

**Fig. 3.4:** Kinematics of the wing. Grey line: Wing excursion $\Phi$. The wing excursion follows a sinusoidal curve with a peak-to-peak amplitude of $64^\circ$. Solid lines: Geometric angle of attack. During upstroke, the geometric angle of attack is adjusted so that the effective angle of attack equals zero at 75%-span of the wing (feathering). During downstroke, the geometric angle of attack is fixed to $0 \pm 1^\circ$. Dashed lines: Effective angle of attack at the wing tip at the corresponding $St$. Grey vertical lines indicate the time steps where 3D flow velocity information was acquired.

Simplifies the experimental setup. A recirculating flow tank with a test section of $50 \cdot 25 \cdot 25$ cm was used. The flow was conditioned and laminarized upstream of the test section by several stages of honeycomb flow straighteners. A constant flow velocity ($U_f$) of 0.46 m/s was applied for all measurements. Both the excursion angle ($\Phi$) and the geometric angle of attack ($\alpha_{geo}$) of the wing (see Figure 3.3) were controlled throughout the wing beat cycle (see Figure 3.4), using a custom flapping device with two degrees of freedom (for more details, see Chapter IV).
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The Reynolds number is calculated as

\[ \text{Re} = \frac{v_{\text{tip}} \overline{c}}{\nu} \]  

where \( \overline{c} \) = mean chord of the wing, \( \nu \) = kinematic viscosity of the fluid and the mean wing tip velocity

\[ v_{\text{tip}} = \sqrt{(2\Phi bf)^2 + U_f^2} \]

where \( b \) = wing span, \( f \) = flapping frequency.

In the experiments, \( U_f \) is constant and only the flapping frequency is altered to meet the target Strouhal number. As a result, the Reynolds number is in the range of \( 2.2 \cdot 10^4 < \text{Re} < 2.6 \cdot 10^4 \) in the current study.

The dimensionless Strouhal number relates the product of vortex shedding frequency and wake height (indicated by the wing tip amplitude, Taylor et al., 2003) to the velocity of the free stream, and is calculated as

\[ St = fA/U_f \]

where \( A \) = peak-to-peak amplitude of the wing.

Strouhal numbers of 0.2, 0.3 and 0.4 were tested, which coincide with the relatively narrow range of \( St \) reported for flying animals in forward flight (Taylor et al., 2003). This range of \( St \) corresponds to a reduced frequency \( (k = 2\pi fc/U_f) \) of \( 0.19 < k < 0.38 \).

FLOW FIELD RECORDING AND ANALYSIS

Due to the highly three-dimensional flow on flapping wings, all three velocity components of the fluid in a volume of 160 \( \times \) 160 \( \times \) 160 mm around the flapping wing were acquired using DPIV. A high-speed camera (A504k, Basler AG, Ahrensburg, Germany, effective resolution = 1024 \( \times \) 1024 pixels) was used together with a 5 W constant wave diode pumped solid state laser emitting light with a wave length of 532 nm (Snoc electronics co., Ltd, Guangdong, China). The laser beam was conditioned using cylindrical and spherical lenses to form a light sheet with a thickness of 1.5 mm. The camera was equipped with a 50 mm lens (Nikkor, f/1.2, Nikon, Tokyo, Japan) and the sensor plane was parallel to the laser sheet. The water was seeded with neutrally buoyant particles (diameter = 57 μm, polyamide, Intelligent Laser Applications GmbH, Jülich, Germany).

A custom DPIV tool developed for this study (PIVlab 1.31, BSD license, see Chapter II) was used to analyze the image data. The cross-correlation was performed in three passes with decreasing window size (iterative multi-grid window deformation technique, Raffel et al., 2007, final window size = 34 \( \times \) 34 pixels with 50% overlap), yielding 59-59 vectors per image. The DPIV data was validated in two successive steps. First, a window velocity filter (global histogram operator, Raffel et al., 2007) was applied to remove vectors with
implausible data. Subsequently, a relatively tolerant standard deviation test was applied, rejecting vectors with a magnitude greater than eight standard deviations of the mean vector magnitude. In total, 0.18% of the vectors in the time-resolved test volume were rejected. The velocity field was smoothed to reduce DPIV-inherent noise and missing data was interpolated in a single step using a robust penalized least squares method (Garcia, 2010). A stack of 59 parallel DPIV slices through the test volume was captured from two perpendicular directions (see Figure 3.5). This procedure results in a 3D Cartesian grid with 59·59·59 nodes and the full UVW velocity information at each point. The spacing between the points is 2.656 mm in all three dimensions, in total 205,379 UVW vectors are captured in the test volume for each time step, each Strouhal number and each wing type.

In total, 35 time steps were captured during one beat cycle of the wing; 10 steps during the upstroke and 25 steps during the downstroke. The exposure of the camera was
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synchronized to the excursion of the wing; at each time step a double image with $\Delta t = 2$ ms was captured. The highly periodic quality of the flow pattern made it possible to record data for a given stroke phase at separated wing beats. Preliminary tests have shown that the flow field was already fully developed after one beat cycle; hence the data capture was launched after two completed beat cycles. Five consecutive full beat cycles were captured for every DPIV slice, hence all data reported in this study is the mean ± s.d. of five samples.

The image distortion introduced by the variable depth of the water column between camera and laser sheet was accounted for by transforming the velocity maps accordingly.

Some regions in the DPIV images are occupied by the wing. These regions appear as bright areas in the images and have to be excluded from the flow analyses to prevent self-correlation. Masks for these regions were created by averaging all images from the same stroke phase. As the particles are distributed randomly, but the wing always occupies the same area, image portions occupied by the wing can easily be detected. The images were then prepared for thresholding by applying a 7×7 pixel median filter. The resulting binary mask was subsequently post-processed to minimize the influence of reflection caused by the wing and applied before the DPIV analysis.

Qualitative analyses of the fluid dynamics require a reliable visualization technique that identifies vortical structures in three-dimensional flow. One common visualization technique uses the magnitude of the vorticity tensor to identify vortical structures. Vorticity magnitude is also sensitive to shear, which makes it difficult to discriminate between vortices and shear layers (Poelma et al., 2006). A suitable candidate for vortex visualization is the Q-criterion (e.g. Hunt et al., 1988; Dubief & Delcayre, 2000; Poelma et al., 2006):

$$Q = \frac{1}{2} (|\Omega|^2 - |S|^2)$$

(3.4)

where $\Omega$ = vorticity tensor, $S$ = rate-of-strain tensor (Haller, 2005)

As Dubief & Delcayre (2000) note, $Q$ expresses the balance between local rotation rate (vorticity magnitude) and local strain rate. Regions where the vorticity magnitude exceeds the strain rate show a positive $Q$ value and highlight vortex core structures (Lu & Shen, 2008). Particularly in the direct vicinity of a wall or a wing, the Q-criterion is supposed to perform better in terms of vortex visualization than vorticity magnitude by itself (Lu & Shen, 2008). To further support the correct identification of vortices, it was checked whether the flow follows a circular pattern either by releasing streamlines (Robinson et al., 1989), or using line integral convolution (LIC, Cabral & Leedom, 1993).

**DPIV Uncertainty**

Digital particle image velocimetry measures the displacement of groups of particles within a certain time period $\Delta t$. The uncertainty of DPIV analyses therefore consists of two main sources of error: Uncertainty of $\Delta t$ between the double images (timing...
uncertainty), and the uncertainty of the displacement estimation. The timing error of the custom synchronizer (mainly governed by the frequency stability of the oscillator that is used for the microcontroller) is maximally 0.005% (Datasheet PXO, Shenzhen South Star Electronics Co., Ltd.). The displacement error of the DPIV algorithm was estimated with a Monte-Carlo simulation (e. g. Raffel et al., 2007) using synthetic particle images with properties that replicate the experimental situation. The simulation showed that the systematic (bias) error is maximally 0.025 pixels and the residual (rms) error is below 0.01 pixels. Along with a mean displacement of 6 pixels per image pair as in the experiments of the present study, this gives an displacement uncertainty in the range of 0.59%.

CIRCULATION ESTIMATES

To quantify the differences between the flow patterns resulting from different St and wing morphologies, the bound circulation was derived from the flow field. The circulation is proportional to the lift that is generated by a wing (Kutta-Joukowski theorem). This theorem has been applied to two-dimensional (e. g. Anderson, 2007) and three-dimensional (e. g. Birch et al., 2004) steady flow conditions, yielding very good lift estimates. Although strictly appropriate only for steady flow conditions, the proportionality of circulation and lift is also reasonably maintained in highly unsteady flows (Unal et al., 1997). The advantage over direct measurements with force transducers that determine the net force generated by a wing, is the ability to derive the temporal and spatial development of circulation, yielding much more detail. Two methods were tested to derive the spanwise circulation (circulation around the spanwise axis) $\Gamma_z$: A loop integral of the tangent velocity and an area integral of the vorticity (see Equation 3.5).

$$\Gamma_z = \oint_{S_{vort}} v_t \, dS_{vort} = \int_{A_{vort}} \omega_z \, dA_{vort} \quad (3.5)$$

where $S_{vort} =$ circular path around the vortex core, $v_t =$ tangential velocity, $A_{vort} =$ area of the vortex core, $\omega_z =$ spanwise vorticity

Several integration domains (different areas and paths) were tested. The resulting circulation estimate was remarkably consistent (see Fig. 3.6 for an example). Increasing or decreasing the diameter of the circular path ($S_{vort}$) decreased the circulation estimate. The vertical elongation of $A_{vort}$ showed only very little influence on the circulation estimate. For practical reasons, an area integral of vorticity was used to derive $\Gamma_z$. The integration plane was set to be perpendicular to the spanwise axis of the wing throughout the whole flapping cycle. Spanwise circulation ranging from 2% to 116% of the wing span was included in the measurements.

The strength of leading-edge vortices can be quantified by measuring the circulation of the LEV. The position and area of the LEV core was determined using the Q-criterion.
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**Fig. 3.6:** **A:** Spanwise circulation of a flapping wing at mid-downstroke, measured with two different methods. Blue line: Loop integral of tangent velocity. Green line: Area integral of spanwise vorticity. Both methods give very comparable results. **B:** Position of the integration domains (green = area integral, blue = loop integral) within the test area (grey).

as a threshold \((Q > 1200)\). Subsequently, spanwise vorticity in that area was integrated to derive the LEV circulation.
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RESULTS

In the first section of the results, a description of the flow field of the 'standard wing' will be given. The effect of Strouhal number on the flow patterns and on the LEV will be presented. In the next section, the influence of wing morphology will be shown, with a focus on the flow field and consequences for the bound circulation and for the LEV.

PRESENCE OF LEVS ON THE 'STANDARD WING'

The wing creates leading-edge vortices during the downstroke at all St tested. The 3D flow visualization shows that size and temporal development of LEV strongly depend on the Strouhal number (see Figure 3.8). When all other parameters are constant, the Strouhal number is a measure for the local effective angle of attack (see Figure 3.4). This parameter largely influences the flow patterns created by the wing as will be shown in the following sections.

At the very beginning of the downstroke (t = 0.56 T), there is no LEV visible for St = 0.2; a weak LEV appears for St = 0.3; and a very large LEV is present at St = 0.4 (see Figure 3.8, vortices confirmed with Q-criterion / broad vorticity peak / streamlines, see example in Figure 3.7).

According to Helmholtz’s second theorem, a discrete starting vortex is expected to be shed from the wing’s trailing edge at the onset of the downstroke. This vortex becomes visible for the intermediate Strouhal number only: A vortex loop system is formed by the leading-edge vortex, the tip vortex and the starting vortex. At St = 0.2, a discrete starting vortex is not visible. If the Q-criterion threshold is set ten times more sensitive,

Fig. 3.7: ‘Standard wing’, cross section at 50% span at mid-downstroke. Close to the leading-edge on top of the wing, a region with elevated vorticity and streamlines / LIC that spiral into a focus become visible.
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A continuous vortex sheet of weak spanwise vortices becomes visible, indicating the release of a series of weak starting vortices from the trailing edge. A discrete starting vortex is also not visible at $St = 0.4$. Lowering the threshold again reveals, similar to the measurements at $St = 0.2$, that several weaker spanwise vortices instead of a single strong vortex are being shed from the wing’s trailing edge.

The flow field continues to evolve with distinct differences between $St$. At the lowest $St$, the LEV is relatively small throughout the downstroke, and stays closely attached to the upper side of wing until it is gradually shed at the very end of the downstroke (see Figure 3.8). At $St = 0.3$, the vortex keeps being attached to the wing likewise, but at the last third of the downstroke, the outer part of the LEV moves away from the top of the wing, indicating that vortex stability starts to decrease. Nonetheless, no larger eddy structures are shed from the wing before the end of the downstroke. At the highest Strouhal number ($St = 0.4$), vortex stability is no longer maintained. A first vortex tube is already created during the wing rotation along the spanwise axis (pronation) before the actual downstroke starts. This vortex is immediately shed from the wing, forming a double horseshoe vortex in the wake (see Figure 3.8). A new LEV develops when the wing begins with the actual downstroke, but it moves substantially away from the top of the wing. Vortical flow structures in the wake dominate the flow field at $St = 0.4$ throughout the whole downstroke, clearly indicating large scale flow separation and unstable LEVs (see Figure 3.8).

More detail on the development of the LEV is given in Figure 3.9, which shows measurements of the cross-sectional area of the LEV at 2/3 span over the wingbeat cycle: As already indicated by the 3D flow visualization in Figure 3.8, the cross-sectional area of the LEV increases substantially with $St$. At $St = 0.2$, the area of the LEV peaks at about mid-downstroke, where the local flow velocity and the effective angle of attack are maximal. At intermediate $St$, the peak is delayed until about 85% of the wingbeat cycle. After this peak, the LEV diameter decreases relatively quickly. At $St = 0.4$, a vortex already develops during pronation, hence before the actual downstroke starts. The following double peak demonstrates LEV separation and reformation, as described earlier.

**Spanwise flow in the ’standard wing’**

Previous studies of flapping wings came to varying conclusions about the occurrence and importance of spanwise flow for LEV stability in flapping or revolving wings. The spanwise flow component of the wing models was analysed throughout the flapping cycle at a number of positions in the present study, including the core of the leading-edge vortex. Exemplary analyses are shown in Figure 3.10. No prominent spanwise flow component that is limited to the core of the LEV was found. However, there is evidence for a region with an elevated positive spanwise flow component behind and
Fig. 3.8: The 3D flow field of the ‘standard wing’ at different time steps during the downstroke. Left: Strouhal number = 0.2, middle St = 0.3, right: St = 0.4. Q-criterion, threshold = 1200, color coded with spanwise vorticity, and texturized with line integral convolution (LIC).
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Fig. 3.9: Area of the LEV at 2/3 span over wing beat cycle. The area of the LEV is determined in a plane that is always perpendicular to the wing, where $Q \geq 1200$. The size of the LEV increases with St.

below the LEV (see Figure 3.10). These regions of spanwise flow also extend slightly into the vortex core, but seem to originate from behind the LEV. The velocity of spanwise flow increases with St and reaches maximum values of 80% of the free stream velocity. No further indications of a strong axial flow inside the vortex core could be detected in the volumetric dataset or in the raw image data.

Distribution of spanwise circulation in the 'standard wing'

The circulation of the wing is a result of the local angle of attack and the local flow velocity; therefore it depends greatly on spanwise position and on wingbeat cycle (see Figure 3.11 for an example). During the upstroke, the geometric angle of attack of the wing is adjusted to make the wing feather through the fluid. The wing base hence has a positive, and the wing tip has a slightly negative effective angle of attack (see contour lines in Figure 3.11). Therefore, during the upstroke, only the inner part of the wing creates weak positive circulation. Most of the circulation is created during downstroke, as expected: Positive circulation is present on the whole wing. The magnitude of circulation is mostly proportional to the magnitude of the effective angle of attack (see Figure 3.11). Close to the wing tip, the effective angle of attack will actually be reduced in practice, due to the influence of the tip vortex on finite wings (‘induced downwash’). Additionally, the main axis of circulation gradually changes from the z-axis (spanwise) to the x-axis (chordwise), leaving the xy-measurement plane. Hence, the peak of spanwise circulation is located at about 80% span at mid-downstroke. These measurements of spanwise circulation
Fig. 3.10: Spanwise flow component of the ‘standard wing’. Left: XY-plane at 2/3 of the span at mid-downstroke. Right: XZ-plane directly on top of the wing at mid-downstroke. The LEV and other vortical structures are outlined in white. The wing translates from right to left. A strong spanwise flow component inside the LEV could not be detected. Instead, a large region with elevated spanwise flow velocities is located behind the LEV on top of the wing.
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Fig. 3.11: Local spanwise circulation and the effective angle of attack of the ‘standard wing’ at $St = 0.3$. Patches: Total spanwise circulation, every patch represents the average of five measurements. Contours: Effective angle of attack derived from kinematics.

are performed for all wing types and will be evaluated and compared in the following sections.

THE INFLUENCE OF WING MORPHOLOGY

Qualitative flow patterns

As expected from the existing knowledge on the influence of wing morphology, the range of morphological wing parameters that were tested did not radically change the fundamental flow patterns compared to the ‘standard wing’. The vortex system of the wing stays consistent in principle; however several differences concerning the downwash and the LEV stability and size are remarkable (see Figure 3.12 and 3.13). The most striking differences will first be described on a qualitative basis; more quantitative results will be given later in this section.
Modifications of wing thickness do not influence the distribution of downwash remarkably (see Figure 3.12). Downwash is mostly concentrated at the wing tip, where the effective angle of attack and the flow velocities are maximal. Still, wing thickness affects the shape and stability of the LEV (see Figure 3.13). At the lowest St, the thick wing creates a smaller LEV than the thin wing. This is less obvious for the intermediate St, however, the LEV on the thin wing seems to move slightly further away from the wing at the tip, indicating the onset of large scale flow separation. At St = 0.4, remarkable differences in the wake can be identified. Here, the thin wing creates two horse-shoe vortices at the trailing edge, indicating an unstable LEV that has been shed from the wing before. These vortices do not appear as explicitly in the wake of the thick wing.

Wing camber influences the qualitative flow patterns even more. Generally, the highly cambered wing has a different downwash distribution along span than the non-cambered wing: At the wing base, the highly cambered wing has higher downwash velocities than the other wing types. In the non-cambered wing, downwash is more concentrated towards the wing tip (see Figure 3.12). Additionally, camber influences the shape and size of vortices in the 3D flow field. At the lowest St, a LEV hardly appears on the highly cambered wing, in contrast to the non-cambered wing, which creates a relatively large LEV. The same trend reappears at the intermediate St; the LEV of the highly cambered wing stays closely attached to the wing surface, whereas the LEV of the non-cambered wing is quite distorted at the tip and moves away from the wing. The effect of wing camber at the highest St greatly resembles the effect of wing thickness: In the wake of the non-cambered wing, distinct horse-shoe vortices appear, again indicating an unstable LEV. These vortices cannot be found in the wake of the highly cambered wing.

In summary, the qualitative visualization of the flow field reveals the following effects: A reduced wing thickness increases the size of the LEV, but decreases the stability at St = 0.4. Increasing wing camber decreases the size of the LEV and increases vortex stability.

**Leading-edge vortex in detail**

The influence of wing morphology on the formation of a LEV was further quantified by measuring the circulation of the LEV core at 2/3 wingspan at mid-downstroke. Wing morphology and Strouhal number both influence the local circulation of the LEV (see Figure 3.14). The circulation of the LEV increases in all wing types significantly with St (Lord Test, $\alpha = 0.05$, Kesel et al., 1999), indicating that the size of the LEV relates positively to the effective angle of attack and the resulting flow velocity. Wing morphology does additionally affect the strength of the LEV, as indicated earlier by the 3D visualization of the flow field. The LEV created by the thin wing is significantly stronger than the LEV on the thick wing for all except the highest St (see Figure 3.14). On average, the LEV produced by the thick wing is by $16 \pm 12\%$ weaker. The effect of wing thickness is however not as pronounced as the effect of wing camber. In all cases, the highly cambered wing
Fig. 3.12: The qualitative influence of wing morphology at 78% of the wing beat cycle. Downwash isosurfaces ($U_y > 0.33 \cdot U_f$). Smaller downwash velocities do not appear in this illustration.
Fig. 3.13: The qualitative influence of wing morphology at 78% of the wing beat cycle. Vortices ($Q > 1200$). Weaker vortices do not appear in this illustration.
The influence of wing morphology

**Fig. 3.14**: Circulation of the LEV (dark colors) compared to the total circulation (light colors) for different St and different wing morphologies at 2/3 span and mid-downstroke. The effect of wing camber is more pronounced than the effect of wing thickness. The relative importance of the LEV increases with St. The circulation of the LEV was determined by integrating vorticity at the leading-edge region in the xy-plane, where Q > 1200.

creates a significantly weaker LEV than the non-cambered wing. This effect does only vary little with St. The highly cambered wing creates a LEV that is on average 30 ± 7% weaker than the LEV created by the non-cambered wing. Wing morphology does not only influence the strength of the LEV, but also the total bound circulation at 2/3 span, as can be seen in Figure 3.14 (bars in light colours). The thin wing has a higher total bound circulation than the thick wing, which agrees well with the increase in the strength of the LEV. In contrast, the non-cambered wing has a lower total bound circulation, although the LEV was shown to be stronger. This will be explained in the discussion.

It is interesting to relate the circulation concentrated in the LEV core to the total bound circulation of the same wing section. Such a ratio is indicative for the relative importance of the LEV to create lift. The fraction of total circulation concentrated in the LEV increases with St from 37 ± 9% to 60 ± 11% to 72 ± 8% when averaged over all wing types (see Figure 3.14). These numbers confirm that the Strouhal number is largely responsible for the relative contribution of the LEV to the total lift.
Fig. 3.15: Mean spanwise circulation ($\Gamma_z$) during the downstroke for all wing types under test.

**Total bound circulation during downstroke**

Further quantitative insights into the influence of wing morphology were obtained by measuring the average spanwise circulation ($\Gamma_z$) of the whole wing during downstroke. $\Gamma_z$ increases significantly with $St$ (see Figure 3.15). The slope of this increase does not depend on wing morphology; all wing types show a very similar trend. Within the range of $St$ that was tested, $\Gamma_z$ increases almost by a factor of two. Wing morphology has a significant effect on the magnitude of $\Gamma_z$. Increasing wing camber increases $\Gamma_z$ (+19.1 ± 8.5% with respect to the 'standard wing', averaged over all $St$), whereas reducing wing camber to zero largely reduces spanwise circulation ($-19.4 ± 4.6\%$ with respect to the 'standard wing'). It is interesting to note that modifications of wing camber have a more pronounced influence than modifications of wing thickness: The spanwise circulation on the thin wing with the sharp leading-edge is only slightly higher than on the 'standard wing' (+5.8 ± 2.9%). The thick wing creates less circulation than the 'standard wing' ($-7.6 ± 0.4\%$).

Insights into the reasons for the increased $\Gamma_z$ of the highly cambered wing can be provided when visualizing the sectional $\Gamma_z$ over wing span (see Figure 3.16). In this figure, $\Gamma_z$ was normalized, so that the area under the curves always equals unity, and relative differences are emphasized. The sectional circulation is supposed to increase with span due to the positive gradient in the angle of attack and flow velocity. This trend
is clearly visible only for the non-cambered wing (see Figure 3.16). The normalization of the sectional $\Gamma_z$ reveals that for the highly cambered wing, the inner 50% of the wing contribute relatively more to the generation of force. In contrast, in the non-cambered wing, $\Gamma_z$ peaks at about 75% of span, clearly indicating that the generation of force is more concentrated toward the outer third of the wing. Wing camber hence increases the spanwise circulation near the wing base where the effective angle of attack is small (see Figure 3.16), but decreases the circulation at the outer 50% of span. It was shown in Figure 3.14 that this is caused by the weaker LEV on the highly cambered wing.
Chapter III

DISCUSSION

FLOW PATTERNS OF THE 'STANDARD WING'

The three-dimensional, time resolved visualization of the flow around the 'standard wing' reveals that LEVs are generated at all St that were tested. Stable leading-edge vortices are created at a Strouhal number of 0.2 and 0.3, several unstable LEVs dominate the flow field at St = 0.4. Previous studies mainly concentrated on the low Reynolds number flight of insects. The current study demonstrates that stable LEVs can also occur during the flapping flight of birds at higher Re, greatly increasing the maximum attainable circulation and thereby force. Both the structure and the temporal development of these vortices are very comparable to three-dimensional LEVs described for insect flight (e.g. Ellington et al., 1996; Liu et al., 1998; Birch et al., 2004).

The comparability of the lift mechanisms used by birds and insects is further demonstrated by recent studies focussing on the flapping flight of birds (e.g. Hubel & Tropea, 2010; Muijres et al., 2012c; Chang et al., 2013). A robotic goose was tested under very similar conditions (Re = 28, 000; St = 0.17) and it was shown that LEVs develop on the wings during downstroke (Hubel & Tropea, 2010). The wing was equipped with an airfoil where wing thickness and camber are very similar to the 'standard wing'. However, the LEVs that developed on the wings of the robotic goose were reported to be unstable after mid-downstroke, which is different from the results of the present study. Although the aspect ratio of the wings differs slightly between the studies, this does probably hardly influence the flow stability (Usherwood & Ellington, 2002b). A more plausible explanation might be the difference in the effective angle of attack. Due to the similarity of the Strouhal number of both studies, the induced angle of attack is expected to be very similar too. In the experiments of the present study, a geometric angle of attack of 0° ± 1° was chosen. The study of Hubel & Tropea (2010) used a geometric angle of attack of +8°, leading to a much higher effective angle of attack right at the beginning of the downstroke (the effective angle of attack at the beginning of the downstroke amounts already 38% of the maximal effective angle of attack that will be attained at mid-downstroke at mid-span). As Bomphrey et al. (2005) summarizes from practical and theoretical experiments, a LEV on a flapping wing is not shed if the duration of the downstroke is short enough to prevent excessive vorticity accumulation in the LEV. But when the geometric and effective angle of attack is large right from the beginning of a downstroke, it is likely that too much vorticity is integrated into the LEV over time, and the size of the LEV exceeds the critical limit, initiating vortex shedding as in the study of Hubel &
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Tropea (2010). Therefore, the Strouhal number per se is not a good predictor for LEV stability if other factors – such as the geometric angle of attack – are not constant.

It has been shown that stable LEVs develop at \( St = 0.2 \) and \( St = 0.3 \) without the need for a spanwise flow component inside the LEV core. This flow component in the core was assumed to be essential in flapping flight (e.g., Ellington et al., 1996; Willmott et al., 1997). Now, a number of indications question the necessity of spanwise flow, as several stable LEVs in the absence of a strong spanwise flow component in the LEV core were discovered (Birch & Dickinson, 2001; Srygley & Thomas, 2002; Thomas et al., 2004; Bomphrey et al., 2005). However, a volume with elevated spanwise flow velocities behind the LEV, as demonstrated in the present study, is common in flapping flight (e.g. Birch et al., 2004; Poelma et al., 2006). The proximity of this region to the LEV might contribute in draining vorticity into the wing tip vortex (Poelma et al., 2006). Spanwise flow in flapping wings is supposed to be driven by ’centrifugal’ acceleration in the boundary layer respectively a spanwise pressure gradient that is caused by a gradient in velocity and angle of attack along the wing (e.g. Ellington et al., 1996). Although there is a large gradient in the effective angle of attack along the wing on a flapping and translating system, the gradient in velocity is small (see Figure 3.17). This is different from a revolving wing or a flapping wing in hovering condition, where both parameters would increase about linearly with wing span. But when flapping at a relatively low Strouhal number, the presence of the free flow velocity decreases the relative velocity gradient along the wing. Due to the lack of a significant velocity gradient, a sufficient pressure gradient along the wing that would drive spanwise flow does not develop. This lack of a pronounced velocity gradient might also limit the peak spanwise velocities measured behind the LEV. A similar conclusion is likewise drawn by Lehmann (2004) to explain the lack of spanwise flow in the flapping flight of some insects.

The contribution of the LEV to enhance aerodynamic lift seems to be generally very important on flapping wings. In the tobacco hawkmoth, the LEV is reported to contribute with 13 to 65% to total lift (Bomphrey et al., 2005). In a robotic model hawkmoth, the LEV contributes at least 65% (van den Berg & Ellington, 1997). At higher Reynolds numbers, the importance does not diminish; hummingbirds gain 15% of lift through the LEV (Warrick et al., 2005), and a passerine about 49% (Muijres et al., 2012c). The measurements of spanwise circulation that are given in the present study show a comparable range of contribution of the LEV to the total lift of 37% to 72%, increasing with Strouhal number. The circulation generated by the wings increases even when the LEV becomes progressively more unstable at \( St = 0.4 \), which agrees with measurements of LEVs that keep on augmenting aerodynamic forces on flapping wings even when they burst (Lentink & Dickinson, 2009). The results about the importance of LEVs in the ’standard wing’ underline the fact that LEVs, even at higher Re, contribute substantially to the circulation, which is proportional to the lift, and they have to be considered as powerful high lift device in slow-speed avian flight.
Fig. 3.17: Gradients in velocity (blue, dashed lines) and effective angle of attack (green, solid lines), derived from kinematics. Each line represents the gradients of the wing at mid-downstroke at $St = 0.2$, $St = 0.3$ and $St = 0.4$ (from bottom to top).

**THE INFLUENCE OF WING MORPHOLOGY**

Wing morphology does significantly influence the aerodynamics of flapping wings. The net effect of wing camber and wing thickness on flapping wings is comparable to the effect in low $Re$ steady-state aerodynamics as presented in the introduction. Still, the observed net effects seem to originate from several different mechanisms in flapping wings.

**Thickness**

Changing the thickness of an airfoil has two geometric consequences: Obviously, wing thickness defines the maximum section thickness of an airfoil. Furthermore, wing thickness also determines the maximum leading-edge radius. The effect of maximum section thickness has been analyzed by Kunz (2003) in steady-state 2D computations at low Reynolds numbers: When set to a positive effective angle of attack, a thick wing develops a much thicker upper surface boundary layer at low $Re$. The low flow velocity behind the position of maximum thickness causes the airfoils to effectively ‘decamber’ (Kunz, 2003). This explains the poor performance of thick wing sections at low $Re$ under steady-state conditions. But it is questionable, whether these results can be applied to flapping wings, where the fluid is mostly separated behind the position of maximum thickness. The present study has shown that the thick wing generates less circulation than the thin wing, but it is likely that it is not an effect of the maximum thickness, but of the nose radius respectively the leading-edge sharpness.

Most of the knowledge about the effect of sharp leading-edges originates from manned aviation, e.g. delta wings that were tested at Reynolds numbers several orders of magni-
tude greater. However, the influence of leading-edge radius depends strongly on Re (Shyy et al., 2008): Under steady-state conditions, at $Re > 10^6$, a wing with a large leading-edge radius can accept a much wider range of angles of attack than a thin wing before flow separation occurs (Shyy et al., 2008). But as the Reynolds number decreases, the more similar the range of acceptable angles of attack becomes and hence the less important leading-edge radius becomes, until the range of acceptable angles of attack is finally equal at $Re = 10^4$ (Shyy et al., 2008). The decreasing importance of leading-edge radius at low Re is also supported by two-dimensional computational studies of rapidly pitching airfoils with varying leading-edge radius (Ramesh et al., 2012). Additional support comes from Usherwood & Ellington (2002a). Their study has shown that leading-edge radius does not significantly influence the amount of lift generated by revolving wings at low Re. But as the study focussed on the measurements of forces only, the reason for this observation could not be determined. At $Re = 10.000$ and $St = 0.16$, but on a purely plunging wing, Rival et al. (2014) have shown that the leading-edge geometry (sharp vs. blunt) influences the diameter of the LEV. On sharp-edged wings, slightly larger LEVs developed due to an earlier onset of the LEV growth. The measurements of the time-resolved, three-dimensional flow field in the present study have shown that the somewhat increased total bound circulation that has been observed on thin flapping wings can be attributed to the increase of the LEV circulation. Thickness was modified quite dramatically (3% to 15%), nevertheless, the effect on LEV circulation (thin wing: 1% to 10% stronger LEV than the standard wing) and also on total circulation (thin wing: 3% to 8% higher circulation than the standard wing) is not as pronounced as expected. It is hence questionable, if the presence of sharp leading-edges should be regarded as the most important wing design parameter responsible for the development of LEVs.

In the light of these results, it can be concluded that leading-edge radius has an effect and that a sharp leading-edge increases the total circulation, but the effect is much less pronounced than at higher Re. Further three-dimensional flow visualizations with flapping wings at $Re > 10^5$ would provide even more insight into the role of the leading-edge radius at low and high Re.

**Camber**

The modification of wing camber has a much more pronounced effect on the circulation. Two consequences that result from the modification of wing camber were identified: First, the strength of the LEV increases significantly by 33 to 61% when wing camber is decreased (highly cambered wing vs. non-cambered wing). Wing camber also has a large effect on LEV strength at the highest Strouhal number, in contrast to wing thickness (see Figure 3.14). Second, wing camber has a pronounced effect on the mean circulation during downstroke (highly cambered vs. non-cambered wing: 28 to 67% increase in circulation). This effect is very much comparable to the effect of wing camber in steady-
flow conditions, where an increase in camber also increases lift (Okamoto et al., 1996). The distinct effect of camber is surprising, as the role of camber in (partly) separated flow conditions – such as under the presence of a LEV – was questioned in previous studies that focussed on force measurements (Dickinson & Gotz, 1993; Usherwood & Ellington, 2002a). In the present study, it was shown that the circulation-enhancing effect of wing camber is concentrated towards the inner 50% of the wing (see Figure 3.16), where the effective angle of attack is relatively small, but the flow velocity is still high, due to the free flow velocity (see Figure 3.17). On a purely revolving, cambered wing as in the study of Usherwood & Ellington (2002a) however, the inner 50% of the wing experience much lower flow velocities due to the absence of wing translation. Hence the lift-enhancing effect of camber will be much less pronounced. The present study has shown that wing camber also limits the strength of a LEV, and therefore any gain in lift that could be achieved by additional LEV circulation. It is therefore plausible, that on a revolving wing with low flow velocities at the wing base, these two effects balance out, and no significant difference in net force can be measured. A revolving wing mimics the aerodynamic situation at mid-downstroke in hovering flight, this situation is aerodynamically different from the slow-speed flapping flight tested in the present study and explains the different conclusions about the effect of camber. The role of camber was also questioned on wings tested under rapid linear acceleration from rest at low Re (Dickinson & Gotz, 1993). The application of camber increases the conventional bound circulation, and decreases the circulation of the LEV – as explained earlier. It might be that the purely translating cambered wing tested by Dickinson & Gotz (1993) creates the same force as the non-cambered wing, because these two effects on circulation balance out. Additionally, their wing was not cambered gradually, but a flat plate was equipped with a sharp bend at 32% of wing chord. Smooth pressure gradients might not develop on such a wing (their importance will be discussed in the next section), inhibiting the separation-delaying effect of wing camber.

The approach presented in the current study – measuring the 3D flow field around a flapping wing – is qualified to analyse the effect of wing camber in detail. Mapping the full flow field is necessary, as the effect of wing camber depends on spanwise position and increases conventional circulation while decreasing the LEV circulation at the same time. Force measurements are not capable of distinguishing these effects.

**Pressure distribution**

An explanation for the effect of wing camber and wing thickness on the strength of the LEV can be given when looking at the chordwise distribution of pressure coefficients. The pressure distribution along the topside of an airfoil largely determines the occurrence of flow separation (Kunz, 2003; Anderson, 2007). If the pressure coefficient rapidly increases behind the leading-edge of a wing, an adverse pressure gradient is generated.
As soon as this gradient becomes too large, the kinetic energy of the fluid will not suffice to keep the fluid following the contour of the airfoil. The flow detaches at the leading-edge forming a LEV that is stable or will be shed, depending on the circumstances. The approximate pressure gradient for the different wings types under steady-state conditions was modelled with a foil-analysis program (XFOIL v6.94, see Figure 3.18). It is shown that the non-cambered wing and the thin wing create such an unfavourable positive pressure gradient (the pressure increases in the flow direction) already at the leading-edge. This adverse pressure gradient is caused by the fluid not being gradually deflected at the leading-edge. The change in direction is abrupt, creating a large positive gradient at the leading-edge which promotes flow separation (Anderson, 2007) and explains the occurrence of large LEVs on the non-cambered wing and on the thin wing. The highly cambered wing however shows the most favourable pressure distribution to suppress flow separation (lowest adverse pressure gradient). This is in good agreement with the results from this study, although the pressure simulation is based on 2D steady-state aerodynamics at relatively low geometric angle of attack.

**Implications for bird wings**

Wing geometry and wing kinematics of the flapping wing model are much less detailed than their natural counterpart. The uncomplicated design of the experiment makes it possible to draw general conclusions from the effect of wing morphology under the presence of LEVs in slow-speed flapping flight. This is important, since LEVs have been recently shown to play a key role in slow flight in birds (Muijres et al., 2012c; Chang et al., 2013), and more knowledge about the effect of wing morphology is desirable.
Chapter III

Controlled slow-speed flight is daily practice in birds, and it is one of the features of bird flight that impresses most. In slow-speed flight, the wings experience relatively low flow velocities. Lift is proportional to the product of flapping frequency squared, stroke amplitude squared and force coefficients. At the same time, the maximum stroke angle, as well as the maximum flapping frequency of birds is limited due to anatomical or physiological constraints. Therefore, high force coefficients would clearly be beneficial (Lentink & Dickinson, 2009). Force coefficients can be maximized by increasing the total circulation of a flapping wing, e.g. by generating LEVs. The thickness of bird wings can easily go below 2.5% for the outer 33% of a wing (Friedel & Kähler, 2012). Thin and light wings will reduce inertia, and therefore reduce the inertial power necessary to accelerate the wings (Usherwood, 2009). But maybe equally important, they will provide higher and more reliable aerodynamic forces by facilitating the development of LEVs. The present study has also shown that wing camber determines the size of LEVs on flapping wings. Camber can be controlled by birds (Bilo, 1972) and e.g. a lanner falcon in free cruising flight considerably alters camber throughout the wing beat cycle (Friedel & Kähler, 2012). Birds may therefore use a combination of thin wings together with variable camber and wing twist to control the strength or occurrence of LEVs and therefore adapt the force coefficients and to direct the forces according to the current needs. It is likely, that the inner part of the wing (arm wing) and the outer part (hand wing) take different roles in force generation. This has been hypothesized earlier for gliding flight (Videler et al., 2004), and the results from the present study strongly support the idea and deliver additional evidence also for slow-speed flapping flight: The hand wing has a low thickness and low camber (e.g. Biesel et al., 1985; Videler et al., 2004; Videler, 2005) and experiences high angles of attack – features that the present study has shown to facilitate the formation of leading-edge vortices. The arm wing however seems to be optimized for fully attached flow aerodynamics: Here, the effective angle of attack and the ‘local’ Strouhal number are lower, the wing is cambered and has a round leading-edge – these factors hinder the development of LEVs. In between the hand and the arm wing, there are several small feathers protruding from the leading-edge (the alula), that could contribute to separating these two regions where different aerodynamic mechanisms dominate during slow-speed flapping flight.

The results on the effects of airfoil parameters can also contribute to understand the wing design of bats. The thin, sharp-edged membrane wing of bats (Muijres et al., 2008) consists – in analogy to birds – of an arm and a hand wing (Norberg, 1990). The membrane of the arm wing (Plagiopatagium) has a higher extensibility than the other flight membranes, and is supposed to have higher camber during flight than the hand wing (Swartz et al., 1996). It therefore appears likely that bat wings are optimized for generating LEVs on the hand wing (as shown by Muijres et al., 2008) and maintaining ‘conventional’ attached flow aerodynamics on the highly cambered arm wing – similar to what we hypothesize for birds.
Slow-speed flapping flight is only one flight mode that birds master. In normal cruising flight, it is likely that aerodynamic efficiency is maximized. That excludes the generation of large LEVs, because prominent LEVs are considered to decrease the aerodynamic efficiency due to a large increase in drag (e.g. Lentink & Dickinson, 2009).

It can be concluded that birds rely on a wide range of aerodynamic mechanisms in flapping flight (analogue to the conclusions for the flight of insects from Srygley & Thomas, 2002); including aerodynamically efficient mechanisms in cruising flight and force enhancing LEVs in slow-speed flapping flight.