The flapping flight of birds
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Chapter IV

The Effects of Wing Twist in Slow-Speed Flapping Flight of Birds: Trading Brute Force Against Efficiency
To be submitted to a scientific journal

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The effects of wing twist in slow-speed flapping flight of birds: Trading brute force against efficiency
ABSTRACT

Aircraft propellers are usually twisted, allowing the propeller blades to operate at a more or less constant effective angle of attack over the full span. Twist enables the full blade to operate at the angle of attack with the maximum lift to drag ratio, which enhances the propulsive efficiency. Wing twist is sometimes also assumed to be essential in flapping flight, especially in bird flight. For small insects, it has however been shown that wing twist has very little effect on the forces generated by a flapping wing. The unimportance of twist was attributed to the prominent role of unsteady aerodynamic mechanisms. These were recently also shown to play an important role in bird flight. It has therefore become necessary to verify whether wing twist is essential in the flapping flight of birds.

The aim of the study is to compare the efficiency and the aerodynamic forces of twisted and non-twisted wings that mimic the slow-speed flapping flight of birds. The analyses were performed with bird-like wing models that are equipped with different amounts of spanwise twist ($0^\circ$, $10^\circ$, $40^\circ$). The flow was mapped in three-dimensions around the wings using digital particle image velocimetry. The spanwise circulation and the induced drag as well as the lift to drag ratio and the span efficiency were determined from this data.

The results show the development of leading-edge vortices (LEVs) on the non twisted wing at all flapping frequencies, and on the moderately twisted wing at the highest frequency. LEVs did not develop on the highly twisted wing. Twisted wings were shown to generate significantly lower aerodynamic forces than wings without twist. However, twisted wings are more efficient. Efficiency and the magnitude of aerodynamic forces are competing parameters. Wing twist is hence beneficial only in the cases where efficiency is important – e.g. in cruising flight. Take-off, landing and manoeuvring however require large and robust aerodynamic forces to be generated. This can be achieved by flapping the wings with only a small amount of twist which promotes the development of leading-edge vortices and increases the aerodynamic forces substantially. The additional force comes at the cost of efficiency, but it enables birds to perform extreme manoeuvres, increasing their overall fitness.
INTRODUCTION

Wing twist is the torsion of a wing parallel to the spanwise axis, leading to a variation of the geometric angle of attack along span (see Figure 4.1). The propeller blades of fixed-wing aircraft are typically twisted, decreasing the angle of attack at the tip of the blade and therefore compensating for the increasing circumferential velocities along the wing blade (Anderson, 2008). Twist allows the entire propeller blade to operate at a more or less constant effective angle of attack – close to the angle with the maximum lift to drag ratio (L/D, Walker et al., 2009). The individual propeller blade elements will hence produce the least amount of drag for a given amount of lift. This means that on a propeller, the torque is minimized for a given thrust. Hence the ratio of thrust producing power to the mechanical power required to drive the propeller (propulsive efficiency, Anderson, 2008) is increased by the application of twist. But not much can be said about the magnitude of thrust producing power. In this context, the optimally efficient propeller has a uniform inflow (and outflow) velocity over the whole propeller disk, and each blade element operates at the effective angle of attack where profile drag losses are minimal (Gessow, 1948). These optimal effective angles of attack (in terms of L/D) are typically in between 3 and 8 degrees for conventional airfoils, depending on the Reynolds number (Re) and on the specific airfoil properties (Shyy et al., 2008).

Flapping wings are common in nature, and the aerodynamics of revolving propellers and flapping wings has some analogies. In fact, a revolving propeller approximates the aerodynamic situation of a flapping wing during the phase of the up- and downstroke in hovering flight (Usherwood & Ellington, 2002a). The analogy between revolving and flapping wings is often used to explain why the wings of flapping-wing flyers have to be twisted in the same tradition as aircraft propellers: At the wing tips, the lift of a

Fig. 4.1: Wing twist at mid-downstroke in an insect. Wing twist is the torsion of a wing along the spanwise axis, leading to a variation of the geometric angle of attack over wing span. Left: Perspective view. Right: Frontal view.
non-twisted, flapping wing is supposed to diminish due to stall because the effective angle of attack becomes too large (e.g. Herzog, 1968; Nachtigall, 1985). Stall can be suppressed by applying wing twist, and twist is supposed to enable the wings of birds, bats or insects to operate at their ‘optimum’ (McGahan, 1973; Norberg, 1990) or ‘most effective’ (Thomas & Hedenstroem, 1998) angle of attack, in analogy to aircraft propellers. It enables to maintain an ‘appropriate’ (Alexander, 2004), ‘favourable’ (Hubel, 2006) or ‘reasonable’ (Azuma, 2007) effective angle of attack at each wing section. In the flapping flight of insects, the analogy between flapping wings and twisted propellers has been questioned already, because the optimum, respectively the most effective angle of attack is not known for insects (Usherwood & Ellington, 2002a). Aerodynamic efficiency might be one important factor in natural flapping wing propulsion: Efficiency can be maximized by adjusting the effective angle of attack towards the optimal L/D using twisted wings (e.g. Young et al., 2009; Walker et al., 2009). Measurements and simulations of model wings mimicking hovering insect flight at low $Re$ have, however, shown that wing twist does not measurably influence the overall L/D of the wings (Usherwood & Ellington, 2002a; Du & Sun, 2008). In the flight of insects, it is likely that the generation of sufficient lifting force is more important than maximizing aerodynamic efficiency (Usherwood & Ellington, 2002a). Lifting forces can be maximized by operating wings at high effective angles of attack and generating stable leading-edge vortices (LEV): LEVs enhance the aerodynamic force coefficients substantially, but are generally not associated with a high aerodynamic efficiency due to a significant increase of the drag component (e.g. Isogai et al., 1999). LEVs are supposed to occur also in the flight of birds (Videler et al., 2004; Warrick et al., 2005; Hubel & Tropea, 2010; Thielicke et al., 2011; Muijres et al., 2012c; Chang et al., 2013, see Chapter III). Especially in slow-speed flight situations, during manoeuvring, take-off and landing, the enhanced force coefficients are required to enable the generation of sufficient lifting forces under several physiological, anatomical and aerodynamic constraints (Lentink & Dickinson, 2009). In these situations, it is very likely that the aerodynamic efficiency becomes of secondary interest – similar to insect flight. Studies on the effect of wing twist on the flow pattern in the slow speed flapping flight of birds have not yet been carried out. Therefore, the aim of this study is to analyse the effect of wing twist at Reynolds numbers and Strouhal numbers mimicking the slow-speed flight of birds. The focus of the present study is on the three-dimensional flow patterns that are generated on and behind wings at several flapping frequencies and with different amounts of twist. Furthermore, the aerodynamic efficiency and the circulation that can be attained with twisted and non-twisted wings is analysed and the biological relevance of the findings for the slow-speed flapping flight in birds is discussed.
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METHODS

WING MODELLING

Physical wing models with different amounts of twist are used to study the flow field in a water tunnel using digital particle image velocimetry (DPIV). The airfoil geometry data used for modelling the wings were derived from measurements of a pigeon in free gliding flight (Biesel et al., 1985) and three-dimensional measurements of dissected wings (Bachmann, 2010, for more details, see Chapter III). The data were used to generate NACA 4-digit-modified-series airfoils (e.g. Ladson et al., 1996) for the wing models. The wings are equipped with a constant camber of 5% at 37% of the chord. Maximum thickness is located at 17% of the chord, the maximum thickness decreases linearly from 10% (wing base) to 4% (wing tip). Additionally, the nose radius was modified with wing span (base: 1; mid-wing: 0.5; wing tip: 0.1; where 1 denotes the radius equal to the original nose radius, and 0 denotes a sharp leading-edge), as indicated by the airfoil geometry data of the pigeon (Biesel et al., 1985; Bachmann, 2010). The single wing aspect ratio \( AR = \frac{b}{c_w} \), where wing span \( b = 120 \text{ mm} \) and mean chord \( c_w = 43.75 \text{ mm} \) of the models is 2.74. The wings are mounted on a 3 mm steel rod, located at 30% of the chord. The wing base is located 12 mm away from the two-degrees-of-freedom (2-DOF) joint, increasing the effective wing span to 132 mm (see Figure 4.2). Three wing models with different amounts of linear twist along the span were designed: The non twisted wing has 0° twist, the moderately twisted wing is equipped with 10° of twist, and the highly twisted wing is equipped with 40° twist (see Figure 4.3).

The wings are equipped with a fixed amount of wing twist and do not adapt to changes in local velocities throughout the wing beat cycle. The results presented here can be seen as a first step and additional experiments with adaptive wing twist may have to follow in future studies. The models were printed with a high resolution 3D printer (ZPrinter® Z310, layer thickness 0.1 mm, resolution 300 · 450 dpi, Z Corporation, Burlington, USA) and the final wing models were casted with transparent epoxy resin (Epoxy casting resin waterclear, Poxy-Systems® by R&G, Waldenbuch, Germany, refractive index 1.53). Due to the refractive index being reasonably similar to water, flow measurements can be performed in the direct vicinity of the flapping wings without shadows.

FLOW TANK AND KINEMATICS

All measurement were performed in a recirculating water tunnel with transparent walls (test section = 250 · 250 · 500 mm, for more details see Chapter III), allowing to visualize the flow from different views. The flow velocity was constant for all measurements.
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**Fig. 4.2:** Flapping robot. Servomotor 1 drives the wing by means of an eccentric, servomotor 2 controls the geometric angle of attack.

**Fig. 4.3:** A: Planform of the wing models. B: non-twisted wing. C: moderately (10°) twisted wing. D: highly (40°) twisted wing.
U_f = 0.46 m/s). The wing was driven by a flapping mechanism that consists of two mechanically and electronically coupled servomotors (see Figure 4.2). The excursion angle of the wing and the geometric angle of attack were controlled throughout the wing beat cycle and synchronized trigger signals were sent to the high speed camera. The wing moves sinusoidally in a stroke plane set to 90° with respect to the oncoming flow. The beat cycle starts with the upstroke, where the interaction of the wing with the fluid was minimized by adjusting the geometric angle of attack in order to minimize the mean effective angle of attack of the wing (see Figure 4.4 for the definition of angles and velocities on a flapping wing). The downstroke was performed with a constant geometric angle of attack (α_geo) of 0° ± 1° at the wing base.

The Strouhal number St = fA/U_f determines the ratio between the flapping velocity, which is induced by the wing flapping at the frequency f with the amplitude A, and the forward velocity U_f. Three different Strouhal numbers (St = 0.2; 0.3; 0.4) are analysed, which are typically found in the flapping flight of birds (Taylor et al., 2003).

Wing twist alters the geometric angle of attack with wing span, and therefore adjusts the effective angle of attack (α_eff). The effective angle of attack for the different wing types and St during downstroke was determined using:

\[
α_{\text{eff}}(t, r) = α_{\text{geo}}(t, r) - α_{\text{in}}(t, r)
\]

where t = time; r = radius of a wing element; α_{in} = inflow angle, calculated as:

\[
α_{\text{in}}(t, r) = \arctan\left(\frac{rω(t)}{U_f}\right)
\]

where \(ω\) = angular velocity of the wing.

The Reynolds number (\(Re = \frac{v_{\text{tip}}E}{\nu}\)), where \(ν\) is the kinematic viscosity) varied slightly with St, and is in the range \(2.2 \cdot 10^4 < Re < 2.6 \cdot 10^4\).

FLOW FIELD RECORDING AND ANALYSIS

The flow was visualized using polyamide tracer particles with 57 μm diameter (density = 1016 kg/m³, Intelligent Laser Applications GmbH, Jülich, Germany) and a 5 W constant wave DPSS laser (Snoc electronics co., Ltd, Guangdong, China). Spherical and cylindrical lenses were used to create a laser sheet with a thickness of about 1.5 mm. The flow was filmed using a high speed camera (A504k, Basler AG, Ahrensburg, Germany) set to a resolution of 1024 × 1024 pixels. Camera exposure was synchronized to the wing excursion with an optomechanical trigger that initiated the exposure of the first image. The second image of the DPIV image pair was triggered with a custom delay system after exactly 2 ms, which gave a mean particle displacement of 6 pixels. The particle density in the images was \(5.80 \pm 0.48\) particles per interrogation area (n = \(7.4 \cdot 10^3\)), and the particle image diameter was \(3.8 \pm 1.6\) pixels (n = \(1.8 \cdot 10^6\)) – conditions that are in the optimal...
range for PIV analyses (see Chapter II). The contrast in the images was enhanced prior to analysis using contrast limited adaptive histogram equalization (CLAHE, Pizer et al., 1987).

In most cases, the wing model appeared in the camera images. The position of the wing was extracted from all recordings to create a three-dimensional mask (see examples in Figure 4.5) that was applied to the images before the analysis in order to prevent self-correlation (for more details, see Chapter III). A custom DPIV tool (PIVlab v1.31) was used to derive velocities from the images. The tool uses an iterative multi-grid window deformation cross-correlation technique. Three passes with decreasing windows sizes (final window size = 34·34 pixels, with 50% overlap) were sufficient to generate precise velocity maps in the two-dimensional test section (size = 160·160 mm, yielding 59·59 vectors, vector spacing = 2.656 mm). The displacement map was validated and missing data were interpolated (for more details see Chapter III).

Five successive downstrokes were recorded. PIV slices were captured from two directions (see Figure 4.6), 59 positions with a distance of 2.656 mm were captured for each the vertical and the horizontal planes. Data acquisition at different planes was enabled without the need for re-calibration by displacing the camera and the laser sheet at the same time (for more details see Chapter III). Due to the highly periodic nature of the flow, the planes could be captured at separate stroke cycles. The combination of the velocity data gives a three-dimensional representation of the flow in a test volume of 160·160·160 mm around the wing. The resulting Cartesian grid (59·59·59 points) contains the full three-dimensional velocity information at each point.

Vortices were visualized with iso-surfaces of the positive second invariant \( Q \) of the velocity gradient tensor, a scalar quantity that reliably detects vortical regions without
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Fig. 4.5: Wing positions as they were extracted from the PIV recordings to generate 3D masks. Yellow: Data from the xz plane. Blue: Data from xy plane.

Fig. 4.6: Several cross-sections through the test volume were captured from two directions. **A:** 59 sections in the xz plane capture u and w velocity components. **B:** 59 sections in the xy plane capture u and v velocity components. Data from both directions were combined, yielding a three-dimensional representation of the flow field. The black arrow indicates the direction of the oncoming flow, the red arrow indicates the stroke plane.
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being prone to shear (e.g. Hunt et al., 1988, for more details see Chapter III). Vortices are present if streamlines or a texture generated via line integral convolution (LIC, Cabral & Leedom, 1993, which is functionally equivalent) circle around a focus when viewed from a frame of reference moving with the vortex (Robinson et al., 1989). The focus must coincide with a broad peak in vorticity and $Q$. This vortex is defined as leading-edge vortex, if it is located on top of the wing and close to the leading-edge and if a region with reversed flow exists on top of the wing.

The circulation along the spanwise axis of the wings was calculated by integrating spanwise vorticity in the xy-plane for each wing section. The results were very consistent compared to an alternative approach, the integral of tangential velocity along a loop around the wing in the xy-plane (for more details see Chapter III). The approach of Birch et al. (2004) to derive sectional lift is followed, which is based on the circulation theorem. This theorem is normally appropriate only for steady flow conditions in two-dimensional flows, but has been shown to give reliable results for similarly unsteady flows at comparable $Re$ (Unal et al., 1997). The sectional circulatory lift at mid-downstroke $L'_{circ}$ is calculated from the product of fluid density, free flow velocity and local spanwise circulation:

$$L'_{circ}(z) = \rho U_f \Gamma(z)$$  \hspace{1cm} (4.3)

where $\rho =$ density, $z =$ spanwise position, $\Gamma(z) =$ spanwise circulation at mid-downstroke.

Integrating $L'_{circ}$ over wing span gives the total circulatory lift ($L_{circ}$). As only spanwise circulation is included in this lift estimate, the real lift of the wings will be underestimated (Birch et al., 2004; Poelma et al., 2006). Due to the identical planform, airfoils, kinematics and experimental conditions of the wing types that are tested, the relative errors are expected to be constant. Hence, the results are nondimensionalized with respect to $L_{circ}$ of the 'standard experiment': the non twisted wing at $St = 0.3$. The induced drag (drag due to lift, Anderson, 2007) was estimated by assuming a momentum balance upstream and downstream of the flapping wing (e.g. McAlister et al., 1995; Giles & Cummings, 1999):

$$D_{ind} = \frac{1}{2} \rho \int_A ((v^2_{down} + w^2_{down}) - (v^2_{up} + w^2_{up}))dA$$ \hspace{1cm} (4.4)

where $v_{up}$ respectively $w_{up}$ represent the vertical respectively spanwise velocities upstream of the wing and $v_{down}$ respectively $w_{down}$ represent the velocities downstream of the wing in the yz-plane.

The results (again nondimensionalized with respect to the non twisted wing at $St = 0.3$) were used to calculate the ratio of circulatory lift to induced drag ($L_{circ}/D_{ind}$). Due to the nondimensionalization, the non twisted wing has a $L_{circ}/D_{ind}$ of unity. This ratio can be interpreted as a relative measure for aerodynamic efficiency, analogous to the $L/D$ of fixed wings. Note that profile drag and additional sources of lift are ignored in $L_{circ}/D_{ind}$. 
Another common measure for aerodynamic efficiency, that has also been applied to flapping flight of insects (e.g. Bomphrey et al., 2006), bats (Muijres et al., 2011, 2012b) and birds (Muijres et al., 2012b), is the span efficiency ($e_i$, for details, see Bomphrey et al., 2006; Henningsson & Bomphrey, 2011):

$$
e_i = \frac{4}{\pi b^2} \left( \frac{\int_{-b/2}^{b/2} v_{\text{down}}(z) \sqrt{b^2 - 4z^2} dz}{\int_{-b/2}^{b/2} v_{\text{down}}^2(z) \sqrt{b^2 - 4z^2} dz} \right)^2 \tag{4.5}$$

where $b =$ wing span.

The span efficiency relates the ideal induced power required to generate a certain amount of lift to the real induced power that is required. The 'ideal wing' (with an elliptic distribution of circulation and a uniform downwash behind the wing) requires the minimum possible induced power (Bomphrey et al., 2006), and has a span efficiency of unity. Any deviation from the uniform downwash will increase the induced power, and therefore decrease span efficiency.

Statistical tests for the equality of means are conducted following the recommendations in Lozän & Kausch (1998) and Kesel et al. (1999) with a significance level of 5%. A Lilliefors test is used for testing normal distribution.
RESULTS

The effective angle of attack of the three different wings during downstroke was determined for the three Strouhal numbers tested using basic trigonometry. In most cases, the theoretical effective angle of attack peaks at the wing tip at mid-downstroke (see Figure 4.7). The non twisted wing experiences the highest effective angles of attack and also the highest gradients. In the twisted wings, the peak effective angles of attack are reduced by $10^\circ$ respectively $40^\circ$. Wing twist ‘overcompensates’ the inflow angle in the highly twisted wing at a Strouhal number of 0.2, resulting in a negative effective angle of attack at the wing tip (see Figure 4.7).

The 3D flow field is captured by recording 2D slices from two different directions. These slices cannot be captured at the same time, which is a potential source of error if the flow is not perfectly periodic. However, taking a phase average of five frames does not substantially alter qualitatively or quantitatively, but it does slightly reduce noise (see Figure 4.8). Therefore, all the following measurements and figures are the mean ± s.d. of five measurements.

First, two-dimensional cross-sections are checked for the existence of vortices. The cross-sections in the xy-plane at 2/3 span reveal the existence of leading-edge vortices on some of the wings (see Figure 4.9). Both the magnitude of vorticity (see colour map) and the induced flow velocities (see vector scale) increase with St and decrease with twist. The non twisted wing creates LEVs at all St: At St = 0.2, the LEV is small and very close to the wing surface, but increases in size at St = 0.3. At St = 0.4, the LEV has grown remarkably and shifts away from the wing substantially, indicating large scale flow separation. The moderately twisted wing generates a LEV only at St = 0.4. At this Strouhal number, the centre of the vortex is located on top of the wing, indicating a region

![Graphs showing effective angle of attack vs. wing span at different St values](image)

**Fig. 4.7:** Effective angle of attack as a function of wing span at mid-downstroke. Both wing twist and St determine the spanwise distribution of the effective angle of attack.
Fig. 4.8: The effect of phase averaging. The fundamental flow patterns are not affected, but measurement noise slightly decreases. Non twisted wing, St = 0.3, 66% span, mid-downstroke.
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![Image: 2D cross-section at 2/3 span at mid-downstroke. The magnitude of vorticity, as well as the flow velocities increase with St and decrease with wing twist. Spanwise vorticity is shown in colour. The texture is generated using line integral convolution. The inflow velocity is subtracted from the vector map.]

Fig. 4.9: 2D cross-section at 2/3 span at mid-downstroke. The magnitude of vorticity, as well as the flow velocities increase with St and decrease with wing twist. Spanwise vorticity is shown in colour. The texture is generated using line integral convolution. The inflow velocity is subtracted from the vector map.

of recirculating flow. At lower St, there is no recirculating flow on top of the moderately twisted wing. The highly twisted wing does not create leading-edge vortices at any St and the interaction with the fluid is generally very small. A significant circulation of fluid around the wing is hardly generated when St ≤ 0.3.

The three-dimensional analyses provide further insight into the detailed nature of the flow field: Visualizations of the Q-criterion reveal the shape of the vortex system (see Figure 4.10). In the non twisted wing, the LEV increases in size towards the wing tip and merges with the tip vortex. At St = 0.4, the LEV becomes relatively unstable, which is indicated by several vortical structures that separate from the wing. It appears that a LEV is also present on the moderately twisted wing at St = 0.3. But the 2D results presented earlier (see Figure 4.9) have shown that this is not the case, as this vortex fails some of the criteria for a LEV (no recirculating fluid on top of the wing). At St = 0.4 however, the moderately twisted wing creates a stable LEV. The highly twisted wing seems to generate only very weak vortices that do hardly appear in the visualization with the selected threshold for the Q-criterion. The tip vortex – which is a good indicator for the generation of lift on finite wings – is too weak to appear in the visualization except for the highest Strouhal number.

The strong influence of St and twist on the flow patterns is also demonstrated in the visualization of the 3D downwash distribution (see Figure 4.11): In most cases, significant downwash is generated over a large part of the span (the visualization shows isosurfaces for downwash velocities > 0.2 · Ut). Peak downwash velocities are located close to the
inner boundary of the tip vortex. The volume of fluid that is imparted with a significant downwash velocity component becomes smaller in the twisted wings due to the small effective angle of attack. As already shown in the visualization of the Q-criterion, the highly twisted wing has the least amount of interaction with the fluid. Only at the highest $St$, a large volume with downwash velocities $> 0.2 \cdot U_f$ becomes visible. In summary, the volume of fluid with considerable downwash increases with $St$, and decreases when wing twist is applied.

Spanwise flow in the core of the leading-edge vortex is a feature described in several studies that analyse or simulate flapping wings. Significant spanwise flow in the core of the leading-edge vortices can not be found. Instead, some weak positive (from base to tip) spanwise flow on top of the wing and behind the LEV is found (see Figure 4.12). In many cases, there is a positive spanwise flow component close to the wing tip which is caused by the rotation of the tip vortex. A negative spanwise flow component (from
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Fig. 4.11: Downwash at mid-downstroke for the different wings and St tested. The threshold for the iso-surfaces is \( 0.2 \cdot U_f \). The downwash is considerably reduced in the twisted wings.

tip to base) is generated on the top side of the tip vortex. This negative spanwise flow component sometimes extends over the outer half of the wing.

The lift generated by bound vortices ('conventional' bound vortex and leading-edge vortex) is determined by the total bound circulation of the wing. All wing types create a positive circulation at mid-downstroke at all St under test (see Figure 4.13). This might be surprising, as the wing with 40° twist is operating at a slightly negative effective angle of attack at St = 0.2 (see Figure 4.7). However, the zero-lift angle of attack for the tested wing is about -3°, which explains the generation of positive circulation at slightly negative effective angles of attack. The circulation increases considerably towards the wing tip in most cases (see Figure 4.13). Circulation also increases with St, but decreases strongly when twist is applied. An elliptic distribution of circulation over span is desirable to minimize the induced drag for steadily translating, fixed wings. The circulation of the flapping wings departs remarkably from the theoretically optimal elliptic distribution in most cases. Only the highly twisted wing at St \( \leq 0.3 \) shows a distribution of circulation that is comparable to the elliptic distribution (see Figure 4.13). In Figure 4.14, the relative
difference of measured versus elliptic distribution of circulation is plotted over span. Any deviation from zero indicates a deviation from the elliptic distribution. The smallest deviation is found in the highly twisted wing where also the gradient in the effective angle of attack is weakest (see Figure 4.7). Here, the relative deviation from the elliptic distribution increases slightly with St. Both the non twisted and the moderately twisted wing have a comparable relative deviation from the elliptic distribution of circulation (see Figure 4.14). Because the relative difference is comparable, the absolute difference increases with St and decreases with wing twist.

Deviations from the elliptic distribution of circulation will increase the induced drag of the flapping wing. The induced drag was calculated from the yz planes at several x positions using Equation 4.4. In preliminary calculations, $D_{\text{ind}}$ was found to be maximal at mid downstroke at the trailing edge of the wing.
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Fig. 4.13: Spanwise circulation along span at mid-downstroke for the different wing types and St tested. The circulation increases with St. Wing twist leads to a decline of circulation. The deviation from an elliptic distribution is in some cases remarkable.

Fig. 4.14: Relative deviation of the measured circulation from an elliptic distribution of circulation with equal mean circulation. Expressed as a fraction of the mean circulation. The highly twisted wing shows the smallest deviation, whereas the non twisted and the moderately twisted wing both show a similar performance.

In all wings, the nondimensionalized $L_{\text{circ}}$ and $D_{\text{ind}}$ increase with St. But there are considerable differences between the lift and drag created by wings with different amounts of wing twist (see Figure 4.15). The non twisted wing generates the highest forces, followed by the moderately twisted wing. The offset between the lift forces generated by different wing types is very constant. This is not the case for the drag forces. Here, the non twisted wing generates an exceptionally high drag at increasing St. The lowest lift and drag are generated by the highly twisted wing (see Figure 4.15): Compared to the non twisted wing, the highly twisted wing generates between 27.1 - 49.4% of circulatory lift and between 6.3 - 19.7% of induced drag.

Plotting the nondimensionalized data over the mean effective angle of attack ($\alpha_{\text{eff}}$) at mid-downstroke shows that $L_{\text{circ}}$ and $D_{\text{ind}}$ can be modelled with $L_{\text{circ}} = \sin(\alpha_{\text{eff}})\cos(\alpha_{\text{eff}})$ respectively $D_{\text{ind}} = \sin^2(\alpha_{\text{eff}})$ (Dickson & Dickinson, 2004, see Figure 4.16). The agreement between the experimental data and the calculated fit is reasonable and does not depend on the amount of twist of the wing.
Fig. 4.15: Nondimensionalized lift and drag. Both increase with St. Wing twist reduces lift by a factor of up to 2.5 and drag by a factor of up to 6.7. Due to the nondimensionalization, the non twisted wing at St = 0.3 has a L_circ respectively D_ind of unity. All means are significantly different (\(\alpha = 0.05\)).

Fig. 4.16: Nondimensionalized lift and drag vs. the mean effective angle of attack at mid-downstroke. A: Normalized L_circ. B: Normalized D_ind. Red = no twist, green = moderate twist, blue = high twist. Due to the nondimensionalization, the non twisted wing at St = 0.3 has a L_circ respectively D_ind of unity. Solid lines represent least-squares fits: 
\[ L_{\text{circ}} = \sin(\overline{\alpha}_{\text{eff}}) \cos(\overline{\alpha}_{\text{eff}}) \times n + l_0 \]
\[ D_{\text{ind}} = \sin^2(\overline{\alpha}_{\text{eff}}) \times n + d_0 \]
\( n = 1.895; l_0 = 0.1751; R^2 = 0.89; \)
\( D_{\text{ind}} = \sin^2(\overline{\alpha}_{\text{eff}}) \times n + d_0 \)
\( n = 4.828; d_0 = -0.01765; R^2 = 0.93 \)

n accounts for the nondimensionalization, and \( l_0 \) respectively \( d_0 \) account for the non-zero force at zero degrees effective angle of attack of the wings.
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**Fig. 4.17:** \( \frac{L_{\text{circ}}}{D_{\text{ind}}} \) for the different wing types. The highest ratio is achieved with highly twisted wings at low \( \text{St} \). Any increase in the effective angle of attack via twist or \( \text{St} \) reduces \( \frac{L_{\text{circ}}}{D_{\text{ind}}} \). All means are significantly different (\( \alpha = 0.05 \)). Due to the nondimensionalization, the non-twisted wing at \( \text{St} = 0.3 \) has a \( \frac{L_{\text{circ}}}{D_{\text{ind}}} \) of unity.

**Fig. 4.18:** \( \frac{L_{\text{circ}}}{D_{\text{ind}}} \) vs. effective angle of attack at mid-downstroke. Data from all twist angles and \( \text{St} \) is pooled. The solid line represents a least squares fit of the function

\[
\frac{L_{\text{circ}}}{D_{\text{ind}}} = \frac{1}{\tan(\alpha_{\text{eff}} + k) \cdot n}
\]

\( k = 0.1502; n = 0.8733; R^2 = 0.9813 \)

\( n \) accounts for the nondimensionalization. \( k \) accounts for the fact that \( \frac{L_{\text{circ}}}{D_{\text{ind}}} \) is positive for negative effective angles of attack (due to the zero-lift angle being smaller than zero), and \( 1/\tan(0) \) not being defined.

The dissimilar relation of lift respectively drag to \( \text{St} \) and wing twist and has a strong influence on \( \frac{L_{\text{circ}}}{D_{\text{ind}}} \) (see Figure 4.17): The highly twisted wing has the highest \( \frac{L_{\text{circ}}}{D_{\text{ind}}} \) when compared to the other wing types at the same Strouhal number. The ratio increases with twist. Additionally, there is also a strong dependence on \( \text{St} \). An increase in \( \text{St} \) leads to a decrease of \( \frac{L_{\text{circ}}}{D_{\text{ind}}} \) (see Figure 4.17). The mean effective angle of attack \( \alpha_{\text{eff}} \) on the wing at mid-downstroke is positively related to \( \text{St} \) and negatively related to wing twist (see Figure 4.7). Figure 4.18 shows the relation between \( \frac{L_{\text{circ}}}{D_{\text{ind}}} \) and \( \alpha_{\text{eff}} \) including all \( \text{St} \). \( \frac{L_{\text{circ}}}{D_{\text{ind}}} \) decreases substantially when \( \alpha_{\text{eff}} \) at mid-downstroke increases. This trend can reasonably be modelled using

\[
\frac{L_{\text{circ}}}{D_{\text{ind}}} = \cos(\alpha_{\text{eff}})/\sin(\alpha_{\text{eff}}) = 1/\tan(\alpha_{\text{eff}})
\]

(see Figure 4.18).

The superior aerodynamic efficiency of wings that are operating at low \( \text{St} \) and that are equipped with twist has been demonstrated by the measurements of the circulation distribution and by \( \frac{L_{\text{circ}}}{D_{\text{ind}}} \). Further support for the increasing efficiency is derived from the distribution of downwash velocities along span: The optimal wing with an elliptic distribution of circulation will induce a constant downwash velocity along the span (Anderson, 2008). Any deviation from uniformity decreases efficiency. Such a uniform downwash distribution can only be observed for the highly twisted wing at \( \text{St} \leq 0.3 \) (see Figure 4.19). This is in good agreement with the nearly elliptic distribution of
Fig. 4.19: Downwash distribution over span at mid-downstroke directly behind the trailing edge. The highly twisted wing creates the most uniform downwash, followed by the moderately twisted wing. The non twisted wing displays the most unfavourable downwash distribution with the highest gradients from base to tip.

Fig. 4.20: Span efficiency of the wings at mid-downstroke. Span efficiency is generally high, and confirms the trend that was found in $L_{\text{circ}}/D_{\text{ind}}$. Non-significant differences (n.s.) are highlighted ($\alpha = 0.05$).

spanwise circulation (see Figure 4.13 & 4.14). Both the non twisted and the moderately twisted wing deviate largely from the uniform downwash distribution (see Figure 4.19). The deviation grows considerably with $\text{St}$, and the non twisted wing always generates the most unfavourable downwash distribution. Due to large scale flow separation at $\text{St} = 0.4$ (see Figure 4.10), a double peak in the downwash velocity can be observed. These qualitative insights on the downwash distribution can be further specified by comparing span efficiency. Due to some noise in the flow velocities directly behind the trailing edge of the wing (caused by the rolling-up of the boundary layer), the results are less clear than the results of $L_{\text{circ}}/D_{\text{ind}}$ (which are based on integral quantities), but show very similar trends (see Figure 4.20): The span efficiency increases when the wings are progressively twisted. The highly twisted wing has a span efficiency that is very close to unity. There is no clear trend for the dependency of span efficiency vs. $\text{St}$. 

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DISCUSSION

FLOW PATTERNS

Wing twist and Strouhal number considerably influence the flow patterns generated by flapping wings. Vortex growth is related to the rate of change in circulation, which is in turn determined by the effective angle of attack (Nudds et al., 2004). The effective angle of attack is related to the Strouhal number which expresses the ratio of $U_f$ and flapping velocity. Wing twist is the ‘counterpart’ to $St$: It lowers both the gradient along span as well as the magnitude of the effective angle of attack. Leading-edge vortices develop if the effective angle of attack is exceeding a certain threshold. Vorticity accumulates in a LEV over time, supposed that there is no effective vorticity drain (Bomphrey et al., 2005). Previous studies (e.g. Ellington et al., 1996; Willmott et al., 1997; van den Berg & Ellington, 1997) found high spanwise flow components in the LEV which are supposed to drain vorticity away from the wing into the tip vortex and to play a key role in LEV stability. In the present study, the LEVs are stable throughout the duration of the downstroke in most cases, significant spanwise flow in the vortex core itself does not develop, regardless of wing twist. Weak spanwise flow was found only behind the LEV on top of the wing. Here, the fluid is presumably accelerated radially by ‘centrifugal pumping’ (Lentink & Dickinson, 2009). The absence of an effective vorticity drain most likely limits the maximum acceptable rate of vorticity accumulation, which is demonstrated by the large scale flow separation in the non-twisted wing at the highest Strouhal number. We have speculated earlier, that the low velocity gradient over the span of a flapping wing in translation hinders the development of a significant pressure gradient that could drive spanwise flow (see Chapter III). The additional application of wing twist reduces the gradient in angle of attack along wing span even more and further reduces the pressure gradients. It therefore appears plausible that spanwise flow is minimal on twisted wings in translational flow. Wing twist also reduces the effective angle of attack, greatly lowering the rate of vorticity accumulation in the LEV. An effective vorticity drain is therefore not essential for vortex stability.

CIRCULATION AND FORCE

The application of wing twist greatly reduces the amount of total bound circulation (proportional to lift) on the wing. In a study on revolving wings at lower $Re$ ($Re = 8000$, Usherwood & Ellington, 2002a), it was shown that the presence of wing twist does not result in different polar diagrams (lift plotted over drag). Altering the amount of wing twist had the same effect as altering the geometric angle of attack of the wing base.
Thus, lift was shown to be proportional to the effective angle of attack of the wing, no matter what the twist angle was. Unlike the study from Usherwood & Ellington (2002a), the geometric angle of attack at mid-downstroke was not altered in the present study. Instead, the effective angle of attack was altered using two different means: Strouhal number and wing twist. Wings that are flapping at comparable effective angles of attack should generate comparable forces according to the results from Usherwood & Ellington (2002a) on revolving wings. In the present study, the effective angle of attack of the moderately twisted wing at $St = 0.3$ is very similar to the effective angle of attack of the non-twisted wing at $St = 0.2$ at mid-downstroke (see Figure 4.7). Furthermore, the effective angle of attack of the moderately twisted wing at $St = 0.4$ and the non-twisted wing at $St = 0.3$ are very comparable (see Figure 4.7). Despite these similarities, the measurements show that the forces are slightly different (see Figure 4.15). One very likely reason for these different forces is the different size of the LEVs (see Figures 4.9 & 4.10). As mentioned earlier, one parameter that determines the size of a LEV is the time span over which vorticity may accumulate in the vortex. Higher flapping frequencies result in less time for vorticity accumulation and explain the slightly different size of the LEV despite comparable effective angles of attack. Therefore, the results of the present study are in agreement with Usherwood & Ellington (2002a): Also in flapping wings at higher $Re$, the effective angle of attack is the main parameter responsible for the magnitude of aerodynamic forces, together with the duration of the downstroke. Wing twist per se is of minor importance for the aerodynamic forces. Further support for this conclusion comes from the trigonometric relation of $\alpha_{eff}$ and $L_{circ}$ respectively $D_{ind}$, that holds for all wing types under test (see Figure 4.16). This relation has been found previously in studies on hovering insects (Dickinson et al., 1999; Usherwood & Ellington, 2002a) and also in a study that included forward flight of insects at very low $Re$ (Dickson & Dickinson, 2004). The present study shows that the trigonometric relation may also be applied to flapping wings at higher $Re$.

$L_{circ}$ increases even if the local effective angle of attack exceeds the stall angle of steadily translating wings (between $8^\circ$ and $15^\circ$, Anderson, 2007). There is no sudden change in forces with the onset of leading-edge vortices. The non-twisted wing has the potential to create much larger lift and drag – simply due to the larger effective angle of attack. $L_{circ}$ and $D_{ind}$ however scale differently, the drag component increases relatively more than the lift component, and this will influence the efficiency.

**Efficiency**

Two measures for quantifying efficiency are used. In addition to the mechanical flight efficiency (related to $L_{circ}/D_{ind}$), the efficiency of lift generation was measured (related to the span efficiency respectively the distribution of circulation). These two independent parameters (Muijres et al., 2012b) both increase substantially with wing twist. The more than 4-fold difference in $L_{circ}/D_{ind}$ between twisted and non-twisted wings (see Figure
4.17) is most likely an overestimation, as other (constant) sources for drag were ignored – these will attenuate the relative differences. It is known that the generation of aerodynamic forces under the presence of leading-edge vortices reduces the mechanical flight efficiency (e.g. Lentink & Dickinson, 2009), and that operating a flapping wing at an $\alpha_{\text{eff}}$ just below the limit of leading-edge separation enhances efficiency (Culbreth et al., 2011). A LEV increases the total aerodynamic force and the gain in lift is accompanied by increased drag due to the loss of the leading-edge-suction force (Polhamus, 1966). Delta-wing aircraft at high Re, but also revolving wings with different amounts of twist at very low Re that generate lift via the LEV, were shown to have a L/D that is inversely proportional to $\tan(\alpha)$ (Polhamus, 1971; Usherwood & Ellington, 2002a; Altshuler et al., 2004). As the results of the present study show, this relation also holds for flapping wings at higher Re mimicking the slow speed flight of birds. In the flapping wings that were tested, any force enhancement that is caused by an increase in effective angle of attack comes at the cost of reduced efficiency. This is not fundamentally different from a finite wing in purely steady conditions (see Figure 4.21). Here, the peak of the maximum force is found at $\alpha \approx 16^\circ$, just before the wing stalls. The highest efficiency (in terms of L/D) is found at smaller angles of attack however (note that in Figure 4.21B, the drag at zero degrees angle of attack was subtracted from the drag measurements. In reality, the optimum L/D will shift towards slightly higher $\alpha$). Efficiency and maximum aerodynamic force hence are competing parameters also under steady flow conditions: Airplanes cannot fly at the maximum L/D in situations that require large forces, like take-off and landing, because efficiency and force coefficients cannot be maximized simultaneously (Anderson & Eberhardt, 2001; Anderson, 2008). In flapping wings, the peak total force coefficient is generated at very high effective angles of attack, because the wing does not stall in the conventional sense. Maximum efficiency and maximum total force are therefore found at very opposed effective angles of attack, and seem to be even more competing parameters than in steady flow conditions.

The efficiency of lift generation was further analysed with two closely coupled measures – the spanwise distribution of circulation and the spanwise distribution of downwash. The latter was used to calculate the span efficiency – a measure for the efficiency of lift generation (Muijres et al., 2012b). The best agreement between elliptic distribution of circulation and the measured circulation was found in the highly twisted wing at low St – a situation where the interaction with the fluid is small and only little lift is generated. Spanwise circulation is positively related to the effective angle of attack (Nudds et al., 2004) and velocity. Both parameters increase with span on a non twisted, flapping wing and potentially yield a distribution of circulation that deviates from the elliptic distribution. To compensate for the increasing effective angle of attack along span, a wing could be equipped with twist, eventually making the effective angle of attack constant along the wing. Even with such a constant effective angle of attack, the velocity gradient along span will still yield a distribution of circulation that is not elliptic. If other parameters are constant, this could only be compensated for by further decreasing the effective angle of
Fig. 4.21: A: Total aerodynamic force $F_{\text{tot}} = (L_{\text{circ}}^2 + D_{\text{ind}}^2)^{0.5}$ (blue) and $L_{\text{circ}}/D_{\text{ind}}$ vs. the mean effective angle of attack. All twist angles and $\text{St}$ are pooled. The total force increases with $\alpha_{\text{eff}}$ and the efficiency decreases with $\alpha_{\text{eff}}$. B: Total aerodynamic force $F_{\text{tot}} = (L^2 + D^2)^{0.5}$ and $L/(D - d_0)$ of the non twisted wing under fully steady conditions, as measured in a wind tunnel. $L/(D - d_0)$ follows a similar trend as in the measurements of the flapping wings. The increase of $F_{\text{tot}}$ stops at 16° (stall). Each parameter is normalized with respect to its maximum value in the measurement.

attack with span by additional twist. This is the case in the highly twisted wing at the lowest Strouhal number: The effective angle of attack at the wing tip is smaller than at the base – it compensates for the higher flow velocities at the wing tip. Subsequently, the distribution of circulation is elliptic, but the circulation and the resulting lift are almost negligible, as lift scales with $\alpha_{\text{eff}}$. From this perspective, it appears questionable whether an elliptic distribution of circulation can be desirable on a flapping wing if it is supposed to generate significant lift. The results of the downwash distribution and span efficiency support these conclusions. Span efficiency increases with wing twist, as the gradient in effective angle of attack diminishes and the downwash distribution becomes more even as a consequence. Despite the large variation of twist and $\text{St}$ that was tested in the present study, the range of span efficiencies appears to be relatively small: The lowest span efficiency is $83.6 \pm 0.8\%$ and the highest span efficiency is $98.6 \pm 0.4\%$. This is comparable to the span efficiencies reported for the flapping flight of several bird species (86% to 95%, Muijres et al., 2012b), indicating that the effective angle of attack in birds might vary similarly as in the present study. It has to be kept in mind that span efficiency is inherently sensitive to noise in the downwash measurements and any irregularities in the downwash distribution. A comparison of the result with other measurements that were taken under different circumstances and with different methods should therefore only be made with caution. The measurements of the present study however support the
idea that twisted wings have the potential to generate lift more efficiently – in addition to
the increase in efficiency caused by the higher $L_{circ}/D_{ind}$.

**TWIST IN NATURE’S FLAPPING WING FLYERS**

Desert locusts are supposed to benefit from the efficiency of attached flow aerodynamics at the cost of reduced peak aerodynamic forces by using twisted wings (Youngh et al., 2009). These organisms are highly migratory, and they might not need the extra forces associated with LEVs that appear at elevated $\alpha_{eff}$, as they are supposed to be less manoeuvrable than other insect species (Bomphrey, 2012). Eventually, the ability of desert locusts to accelerate very rapidly from rest to the minimum flight speed via jumping (Katz & Gosline, 1993) renders the requirement of generating large forces at low flight velocities less important, and allows to use wing twist to increase efficiency. Butterflies are another example where wing twist enhances aerodynamic efficiency, but also reduces peak lift forces during the downstroke (Zheng et al., 2013b).

In the cruising flight of birds, peak lift forces are most likely not of primary importance. Here, energetic efficiency is likely to play a major role due to the high energetic costs and the long duration of cruising flight periods (e.g. Norberg, 1990). Birds can afford to avoid the high drag that would come with the development of leading-edge vortices (Nudds et al., 2004; Park et al., 2012): The application of wing twist helps to find the optimum balance between aerodynamic efficiency and the required aerodynamic forces during cruising. Cruising flight with a close-to-optimal L/D therefore seems to be possible. Furthermore, the gradients in velocity and $\alpha_{eff}$ over wing span are inherently weaker in cruising flight than in slow speed flight. Airfoil shape, wing planform and twist can compensate for some of the gradients in circulation over wing span (e.g. Anderson, 2008). Bird wings are cambered at the wing base and more flat close to the tip (e.g. Nachtigall & Wieser, 1966; Liu et al., 2004). Wing camber increases lift with attached flow aerodynamics (e.g. Okamoto et al., 1996, Chapter III of this thesis), and the spanwise distribution of camber in combination with twist could be a strategy to increase the span efficiency in cruising flight.

The story looks however different in slow speed flight, during manoeuvring, take-off and landing: The selection pressure to avoid being killed by predators is very high in birds: The ability to take-off rapidly and to manoeuvre quickly will decrease the chance of a bird to be killed (e.g. Lima & Dill, 1990; Swaddle & Lockwood, 1998; van den Hout et al., 2010). In predator escape, rapid accelerations require large forces to be generated by the wings. Aerodynamic efficiency does not seem to be an important target of selection in these situations (Curet et al., 2013). According to the results of the present study, wing twist is very disadvantageous when such large forces are required. Furthermore, the ability to fly very slowly just before landing will reduce the chance of injury or wing damage. Keeping the wings perfectly intact is important, as the flight performance during take-off, manoeuvring and escape reactions decreases substantially with damaged wings.
(e.g. Tucker, 1991; Swaddle & Witter, 1997; Chai et al., 1999). As stroke amplitude and flapping frequency in birds are constrained (Lentink & Dickinson, 2009), slow flight requires high lift coefficients. These can best be achieved by operating the wings at high angles of attack. Stall does not seem to be a primary issue on flapping or revolving wings (Usherwood & Ellington, 2002b; Thielicke et al., 2011; Ozen & Rockwell, 2012, Chapter III of this thesis), and lift continues to increase until very high effective angles of attack under the presence of leading-edge vortices. LEVs increase lift and drag at the same time and enable manoeuvres that are essential for bird flight. Despite the implication of the word, the increase in drag does not always need to be disadvantageous. Lift and drag both contribute to the total aerodynamic force. If the stroke plane is set correctly, all of the total aerodynamic force can be used to offset weight. This has been shown previously for the flapping flight of dragonflies: Drag can be used to support three quarters of the weight, and potentially, the required power for flight can be reduced by a factor of two (Wang, 2004). As the results of the present study have shown, this might for a good part also be applicable to the slow-speed flapping flight of birds, as the aerodynamic mechanisms of insects and birds are not fundamentally different.

Wing twist can however be observed on some birds in slow speed flight (e.g. Rosén et al., 2004). Recently, two studies managed to visualize the flow directly around the flapping wings of slowly flying birds (Muijres et al., 2012c; Chang et al., 2013). Prominent LEVs were found, and it seems that wing twist in slow-speed flight is not used to avoid the development of LEVs, but rather to modulate their size and stability and to direct the resultant force. Maybe, the application of wing twist is generally not used to decrease \( \alpha_{\text{eff}} \) at the wing tip, but to increase \( \alpha_{\text{eff}} \) at the inner part of the wing. This would result in high angles of attack and high aerodynamic forces over the full wing – however at the cost of efficiency. Further flow visualizations of the fluid directly around the wings of birds flying at several speeds are highly desirable to validate the results and to get further valuable information on the control of flow separation in birds.
CONCLUSIONS

Wing twist was assumed to be essential in the flapping flight of birds in order to keep the effective angle of attack sufficiently low. It was shown that this is not strictly necessary, and that reducing the effective angle of attack at the wing tip reduces the aerodynamic force – in analogy to the flapping flight of insects. It is likely, that such a reduction in the peak aerodynamic force is undesirable in many situations in avian flight. In slow flight however, the purpose of wing twist might not be the reduction of the effective angle of attack at the wing tip, but the increase of $\alpha_{\text{eff}}$ at the wing base, making the whole wing operate at high effective angles of attack. The mechanical flight efficiency (related to $L_{\text{circ}}/D_{\text{ind}}$) as well as the efficiency of lift generation (related to span efficiency) degrade when $\alpha_{\text{eff}}$ is increased – similar to a wing in purely steady conditions. But even if the aerodynamic efficiency significantly drops, the overall fitness of a bird is supposed to increase due to the ability to generate larger forces.

The ability to modify the force coefficients of the wings via wing twist and the resulting changes in $\alpha_{\text{eff}}$ will largely enhance the flight envelope, making flapping wing locomotion very attractive. From the engineering point of view, the cruising flight of flapping-wing vertebrates might be of secondary interest, because existing fixed wing airplanes already outperform birds in terms of the energetic cost of transporting a unit of weight over a unit of distance (cost-of-transport, Tucker, 1970). In contrast, the manoeuvrability and versatility of avian flapping flight is yet totally unmatched by any technical application and it is an important source of inspiration for researchers and engineers today and in the future.