## 1 ELECTRONIC SUPPLEMENTARY MATERIALS

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8	Canada.
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10	Animals. Seven male Anna's hummingbirds (Calypte anna), euthanized for other studies at the
11	University of California, Riverside, were stored frozen in good condition. After careful preparation,
12	their wings were donated to the Museum of Vertebrate Zoology at the University of California,
13	Berkeley, and subsequently loaned from the University of California, Berkeley (CITES: US-052
14	(A/P)) to Wageningen University (CITES: NL-004) for aerodynamic study. The wings originated
15	from birds for which all animal procedures were approved by the Institutional Animal Care and Use
16	Committee of the University of California, Riverside.
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18	Wing preparation. The hummingbird wings were removed from the (proximal) base of the
19	humerus and dried in fully spread position to resemble wing morphology during hovering flight. We
20	removed minimal amounts of wing material to glue the wing base into a square plastic tube aligned
21	with the innermost secondary feather. The square tube was mounted on a square rod attached to the
22	variable pitch mechanism of the spinner. We then selected $n = 5$ right wings that had least
23	imperfections in the feathers due to wear, molt, and preparation, Supplementary Figure 1a. Each
24	wing's out-of-center mass was carefully counterbalanced with an opposing plastic mount filled with
25	lead fishing weights. Finally, we artificially groomed (preened) the feathers with our fingers and an

entomological pin to close small gaps. When necessary gaps were closed using a minimal amount of
hairspray applied locally with a pin; we sprayed the solution in a cup, soaked the head of the pin in it,
and applied minimal amounts with the pin to fix particular barbs.

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Model wing design. We confirmed similarity of the aerodynamic performance of rectangular model 30 wings (AR = 3.5, Re = 11,000) and *Calypte anna* wings (n = 5, ave AR = 4.1, ave midstroke Re = 4.131 32 14,000), figure 1c. To isolate the effect of aspect ratio on revolving wing performance, we then designed a range of carbon fiber model wings. These wings vary in wing length only and have the 33 34 same rectangular planform, constant chord length, and camber, supplementary figure 2. A recent 35 analysis<sup>1</sup> predicts that stall delay on revolving wings is mediated by rotational accelerations, and that 36 stabilization of the leading edge vortex (LEV) stops beyond a local aspect ratio r/c (local radius, r, divided by chord, c) between 1 and 10, close to 3. We selected aspect ratios (AR = 2-3-4-5-6.5-8-10) 37 that sample this range and the hummingbird aspect ratio range:  $AR = 3.7 \pm 0.3$  std (n = 65). The 38 39 model wings were built up from two 0.2mm carbon fiber plies and had 15mm chord. We selected 6% airfoil camber for good hover performance<sup>2-4</sup>, similar to hummingbird wings<sup>5</sup>. We iterated the 40 airfoil design to ensure the wing was stiff enough and did not flutter within our measurement range. 41 42 Each wing was fitted with a plastic square mount to clamp it onto the spinner and a minimally protruding hooklet at the wing base. This hooklet helped secure each model wing to the spinner with 43 an orthodontic rubber band. We found that hummingbird wings and low aspect ratio model wings 44 45 could be spun without vibration by balancing them using a counterweight (fishing leads attached to 46 plastic mount). High aspect ratio model wings, however, vibrated due to the relatively large eccentric aerodynamic forces at the larger outward radius of gyration of the wing<sup>6</sup>. We therefore tested all 47 48 model wings in pairs, which balances the aerodynamic and inertial forces such that the setup does

49 not vibrate. Each wing pair was carefully balanced by gluing small lead fishing weights at the lower50 surface into one of the plastic mounts.

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52 Wing spinner. We designed a computer-run wing spinner to autonomously control wing tip 53 Reynolds number, Re, (through spinning frequency) and incidence angle,  $\alpha$ , of single wings or wing 54 pairs. Two micromotors (AXi2212/34 and AXi2208/20, Model Motors) with complementing torque 55 ranges powered a single hollow axle, suspended with ball bearings in an aluminum housing. Through the axle ran a non-rotating, servo-actuated push-pull rod to control a variable pitch propeller 56 mechanism fitted with square rods on which the plastic wing mounts could be clamped. The 57 58 micromotors were controlled using an electronic speed controller (M-Drive-18, Motortron System 59 Inc) and a servo board (ServoCenter 3.1, Yost Engineering). The spinner design minimized the distance between the rotation axis and the wing root, d, to 9.5mm. This offset was incorporated in 60 61 our calculation of the target spinning frequencies to maintain constant wing tip Reynolds number  $Re = \rho 2\pi f(R + d)c/\mu$  (air density,  $\rho$ , spinning frequency, f, wing length, R, and dynamic 62 63 viscosity,  $\mu$ ). The dynamic viscosity was calculated based on the measured air temperature using Sutherland's equation<sup>7</sup>:  $\mu = \mu_0 (T_0/T)^{1.5} (T_0 + S)/(T + S)$ , (air temperature,  $T, \mu_0 = 18.27 \text{ ms}^{-2}, T_0$ 64 = 291K, Sutherland's constant for air, S = 120K). The same spinner was used during force 65 measurements and quantitative flow visualization. 66

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Calibration of force measurement. To make reliable static (time-averaged) force measurements,
the spinner was mounted onto an overdamped balancing setup supported by weighing scales (Ohaus
Adventurer Pro, 210g range, ±0.001g), Supplementary Figure 1c. Accuracy of the torque
measurement proved to be the setup's main challenge, as expected based on earlier studies<sup>8,9</sup>, and was
improved greatly by automating the setup, thus minimizing the required handling between

73 measurements. Accuracy was further improved by mechanically isolating the setup on a heavy granite 74 table supported by rubber dampers, and aerodynamically shielding the balance from the propeller 75 wake with clear plastic cowlings rested on separate supports, Supplementary Figure 1b, c. High-76 frequency vibrations from the spinner were damped using rubber-plated motor suspension and 77 averaged out using custom-built silicon oil dampers (10,000 cSt polydimethylsiloxane, Tribolub). We calibrated the force balance statically by using weights to apply lift force along the rotation axis  $(0.3^{\circ})$ 78 79 accuracy) and pure torque around the rotation axis. These weights were hung from wires running 80 horizontally from the setup over pulleys with negligible friction. We applied a pure torque (without 81 net force) by mounting a vertical arm, sticking both upward and downward, onto the spinner. One 82 wire was connected to the upper end of the arm and another wire in the opposite direction to the 83 lower end, to apply identical but opposing forces, resulting in a pure torque. All weights were 84 submerged in paraffin oil (2.4 cSt, Texaco) to prevent them from swaving during the calibration. To 85 account for coupling effects, we applied combinations of lift and torque to build a  $9 \times 9$  calibration 86 matrix with increased resolution around zero lift and torque to accomodate low Reynolds number 87 measurements. These calibrations were repeated five times before and after the measurements. Average calibration bias over all measurement points was 5.0% on torque and 1.0% on lift. We 88 89 separately measured lift and torque generated by the rotating parts, e.g. mechanical friction in the ball 90 bearings and aerodynamic drag on the plastic wing mounts, as well as center of gravity displacement 91 due to servo actuation, and subtracted all these effects from the wing measurements to obtain precise 92 aerodynamic forces.

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94 Force measurements. We measured time-averaged lift and torque on wings spinning at constant
95 Reynolds number and incidence. After a conservative 5 second settling period (determined
96 experimentally), the measured reaction forces were sampled 100 times via USB at 5-6Hz and stored

by custom-built Matlab code (v2009a, Mathworks). Thin wires were connected close to the balance's 97 central pivoting point for power supply (7.4VDC, DPS-2010PFC, Voltcraft) and motor control. The 98 99 model wings were taken through a range of Reynolds numbers (Re = 5,000-25,000, stepsize 4,000) 100 and incidence angles ( $\alpha = -3^{\circ}-60^{\circ}$ , stepsize 1° for  $\alpha < 20^{\circ}$  and 3° for  $\alpha \ge 20^{\circ}$ ). Hummingbird 101 wings were tested at the midstroke Reynolds number during hover (ave Re = 14,000) calculated using 102 measured mean chords and angular velocities assuming a sinusoidal wing stroke<sup>6</sup>. The aerodynamic 103 measurements were repeated 3 times. Every repetition consisted of an upward leg during which 104 incidence was increased till the maximum angle of attack was attained, after which the angle of attack 105 was reduced during the downward leg till it reached the minimum value. These three complete loops 106 enabled us to check for hysteresis effects, which we did not find. The weighing scales measured lift 107 forces ranging between 0.00003N and 5.73N and torques between 0.000013Nm and 0.246Nm. The 108 torque measurement range was limited by motor power (at very high and very low AR,  $R_{\ell}$ ,  $\alpha$ ) and by 109 measurement resolution (at very low AR,  $R_{\ell}$ ,  $\alpha$ ). We obtained 600 measurements per data point for 110 statistical rigor. Since the setup has been calibrated for static measurements, resulting in a static 111 transfer function that relates displacement to force, we checked if the balance attained static 112 conditions. We used the fast Fourier transform (FFT) to compute the dynamic power present in the 113 frequency spectrum below 1Hz (at higher frequencies the power was negligible) in both the lift 114 (Supplementary Figure 3a, c, e.) and torque (Supplementary Figure 3b, d, f.) measurements. Based on this evaluation we disregarded the torque measurements for which the balance was unable to reach 115 116 static equilibrium: at Re = 5,000 and beyond 35° incidence (Supplementary Figure 3b, d, f.). All lift 117 measurements were static and thus accepted, Supplementary Figure 3a, c, e. A single outlying point for the drag coefficient was marked as a dot, Supplementary Figure 4b, 5b, but removed from the 118 Reynolds average (Figure 2). 119

121 Force coefficients. We calculate aerodynamic force coefficients by dividing lift by

1/2  $\rho(2\pi f)^2 SR_2^2$  and drag due to torque by  $1/2 \rho(2\pi f)^2 SR_3^3$  using air density,  $\rho$ , spinning 123 frequency, f, wing area, S, and the radii of second and third moments of area  $R_2$  and  $R_3$ , to account 124 for the velocity gradient along the wing span<sup>6,8</sup>. Lift is defined as the force perpendicular to the 125 stroke plane, neglecting induced flow effects. After checking for hysteresis effects, which we did not 126 find, we averaged the 600 lift ( $C_L$ ) and drag ( $C_D$ ) coefficients measured at each incidence. Zero 127 incidence was defined as the point of zero lift, based on the zero intercept of the  $C_L$ - $\alpha$  curve for 128  $0.05 \le C_L \le 0.50$  for each wing.

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130 Power factor. To compare the aerodynamic power required for hover we compute power factor as a 131 function of incidence,  $PF = C_{\rm L}^{1.5}/C_{\rm D}$ . The amount of weight that can be lifted with a unit 132 aerodynamic power is proportional to this factor<sup>10</sup>. Power factor represents a 'gradient' and therefore 133 amplifies noise in the drag coefficient. A penalized least-squares algorithm<sup>11</sup> was used to smooth the 134 force coefficient curves versus incidence before calculating the power factor and thus limit noise.

136 Particle image velocimetry (PIV). To quantify the velocities in the flow around the wings, we 137 seeded the room with microscopic smoke particles illuminated by laser light captured with a phase locked camera (details are provided in Supplementary Table 1 below). We recorded 20 (model wings) 138 or 25 (hummingbird wings) phase-locked image pairs in 2D planes along the span of the spinning 139 140 wing. We automatically moved the imaging plane along the span using a linear actuator that traversed 141 the spinner and its mounted wing through a laser sheet. Both the laser and the PIV camera were 142 triggered when the wing passed in front of a camera, Supplementary Figure 1b, d. The laser beam 143 was split using mirror optics to illuminate the wing and reduce shadow effects. Image pairs were 144 cross-correlated using DaVis software (v7.4, LaVision GmbH) using a multi-pass cross-correlation

procedure consisting of a first pass on a  $128 \times 128$  pixel grid (0% overlap) and then two passes on a 145 finer 64×64 pixel grid (75% overlap)<sup>12</sup>. Flow measurements were made for all model wings over a 146 range of Reynolds numbers (Re = 5,000-13,000-25,000) and incidence angles ( $\alpha = 15^{\circ}-30^{\circ}-45^{\circ}$ ). One 147 wing of *Calypte anna* was tested at its midstroke Reynolds number (Re = 13,000) at these same three 148 149 incidence angles. We made recordings at 19-22 equidistant spanwise recording stations from wing root to well beyond the tip. Step sizes for the model wings increased from 1.3 to 6.6 mm with aspect 150 ratio; step size was 2.25 mm for the hummingbird wing. Reflections from the spinner as well as the 151 plastic wing mounts were minimized using matte black grease (Zebraline stove polish), and the 152 model wings were coated with matte black spray paint. During postprocessing, images from a 153 simultaneously triggered second camera, under a 35° stereo angle, were used to correct for small 154 trigger errors and match airfoil positions precisely to calculate the average flow field. 155

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Vortex identification. The leading edge vortices are visualized by plotting vorticity. We used a 157 vortex detection scheme to confirm that the visually obvious vorticity concentrations are vortices 158 using the MATLAB vortex identification code of Jones et al.<sup>13</sup>. This implementation of a non-linear 159 160 vortex detection scheme in which the axisymmetric vortex intensity at a point P in the velocity field is defined as  $\gamma(P) = \frac{1}{N} \sum \sin(\theta_M)$  following the work of Graftieaux *et al.*<sup>14</sup>. This identification 161 method is more robust against noise in the PIV recordings<sup>13</sup>. Vorticity concentration and high vortex 162 163 identification levels overlap, demonstrating that the vorticity concentration at the leading edge are 164 indeed a leading edge vortex for all wings tested (Supplementary Figure 8). We thus conclude that our vorticity fields are sufficiently noise-free to detect vortices based on vorticity concentration. 165 166

167 Vortex lift coefficient. The vortex lift distribution was calculated by integrating the vorticity field to 168 determine local circulation,  $\Gamma$ , for a fixed control area intersecting the wing at each spanwise station.

169	We omitted the area below the wing, where the laser illumination was insufficient, from the area of
170	integration. We cut off vorticity below a threshold level based on free-stream vorticity noise
171	measured in front of the wing. From the circulation we computed local vortex lift coefficients as
172	$C_{l} = 2\Gamma/Vc$ using local wing velocity, <i>V</i> , and chord length, <i>c</i> . For the hummingbird wing we used
173	the local wing chord in this computation. The average vortex lift integrated over the full span of each
174	model wing predicted 78-97% of the lift measured with the force balance for model wings at $\alpha$ =
175	30°, and 55%-109% at 45°; for the humming bird wing the calculated fraction was 71% of the
176	measured lift coefficient at 30° and 77% at 45°. The discrepancy between measured and calculated
177	lift is expected, because the control volume integral of the Navier-Stokes equations is only
178	approximated by integrating circulation <sup>12,15-22</sup> .

Table 1. Components of phase-locked PIV setup

Smoke generator	VDP900HZ, HQ power
Laser	Dual SL454-10-OPG, Spectron Laser Systems, flashlamp pumped
	Nd:YAG laser, 532nm, 200mJ/pulse, 13ns pulse duration, 15Hz
	repetition rate
Tachometer for triggering	PLT200, Monarch Instrument
Camera	MegaPlusII ES 2020, Redlake, 30fps, 1600x1200px with 105mm
	zoomlens, Nikkor Micro, Nikon
Linear actuator	custom design, 5mm/stroke ball screw, AMS AM34-420-2-EFB
	stepper motor and AMS MAX-410 controller





Figure S1. Hummingbird wings and spinner setup used for force measurements and quantitative flow 183 184 visualizations. (a) The right wings of five male Anna's hummingbirds (Calypte anna) were used for force measurements; the left-most wing produced a force polar close to the species average and was 185 186 used during PIV measurements. Each wing is glued into a plastic mount that clamps onto the spinner. (b, c) During force measurements the spinner was mounted on a balance pivoting on a 187 188 fulcrum (green) and supported by weighing scales (blue) to measure reaction forces. The setup's 189 center of gravity deliberately almost coincided with the pivoting point. The counterweight is 190 connected below the fulcrum (not shown here for clarity, it consists of a custom D-shaped aluminum 191 connector that fits around the fulcrum). The balance was overdamped to measure time-averaged 192 forces. The spinner was also carefully shielded from propeller secondary flow using a separately supported cowling (clear plastic). This cowling connected to a bottom plate (not visible) supported 193 by side plates that shielded the balance system from air currents. (d) Phase-locked image pairs were 194 195 recorded by a PIV-camera looking along the wing span during the PIV measurements. A second

196 camera under a 35° stereo angle assisted in determining the wing location in the flow field. The

197 spinner was traversed laterally through the laser sheet using a linear actuator (not visible).

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Figure S2. Model wings with aspect ratios 2-10. Carbon fiber model wings were produced by 200 201 ProxDynamics in Nesbru, Norway and used for force measurements and PIV. All wings were 202 originally produced with aspect ratio 10 with constant chord and uniform airfoil. To lower aspect 203 ratio, wing length was reduced using a table saw with a diamond-tipped blade. (a) The airfoil is built 204 up from two 0.2mm carbon fiber plies with 6% camber and 15mm chord length. The airfoil design 205 was iterated to eliminate flutter throughout the measurement range. (b) Each wing is glued into a 206 small plastic mount at the quarter-chord point, which clamps onto the spinner. Small carbon fiber 207 rods protruding from the wing base served as hooklets around which we tied small orthodontic 208 rubber bands to secure each wing to the spinner.

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Figure S3. Low frequency fluctuations in the raw drag coefficient signal indicate measurement 212 limitations at Re = 5,000 and for  $\alpha > 35^\circ$ . The power spectrum of the raw lift (left) and drag (right) 213 coefficient signal (sampling frequency 5-6Hz) was computed using a fast Fourier transform (mean 214 value subtracted; signal reflected at both end points) in the 0-1Hz frequency range, which contained 215 216 almost all power. We calculated the first spectral moment by integrating power × frequency in this 217 range, which represents a frequency-weighted form of kinematic power. The kinematic power 218 contained in these low frequencies indicates whether system dynamics interfered with measurement 219 of setup deflection, which was calibrated to determine aerodynamic forces. The kinematic power of the force coefficient series is non-dimensional. (a, c, e) Average kinematic power in the lift 220

221	coefficient series does not exceed 0.012 for $\alpha = 0-60^{\circ}$ , indicating all lift force measurements were
222	within the steady range of the balance. (b) Kinematic power in the drag coefficient signal is 0.017 $\pm$
223	0.006 around 35° incidence, and increases exponentially beyond acceptable levels at this angle. This is
224	illustrated by the grey exponential fit through the maximum power at each incidence for $30^{\circ} \le \alpha \le$
225	60° ( $C_D = 10^{-3.52+0.0656\alpha}$ , $R^2 = 0.9168$ ). Since the setup was calibrated statically to measure steady
226	forces, we disregarded all drag measurements beyond 35°, because these drag force measurements
227	were within the dynamic range of the balance. The sub-panel shows representative spectra for
228	different angles of attack, above 35° the drag spectra reveal balance dynamics. (d) The kinematic
229	power in the drag coefficient signal is highest for low aspect ratio wings at Re 5,000 both at low and
230	high incidence. Model wings with aspect ratios 2-4 at Reynolds number 5,000 generate the smallest
231	aerodynamic forces in this dataset, defining the range limitation of the setup. We therefore omitted
232	the measurements at Reynolds number 5,000 from the analysis. Open dots plotted in c,d represent
233	Re 5,000; closed dots Re 9,000-25,000. (e, f) Average logarithmic power for all force coefficient
234	measurements at $Re \ge 9,000$ (thick black line: average, area: std, dots: min & max values).



Figure S4. Aspect ratio effect on force coefficients at hummingbird midstroke Re = 13,000 is similar 236 to the Re averaged effect shown in Figure 2. (a-c) Lift, drag and power factor versus angle of attack 237 238 as a function of aspect ratio. Aspect ratio 4 wings combine near maximal lift, and intermediate drag, which maximizes power factor beyond 20°. A single outlying point for the drag coefficient is marked 239 as a dot (and ignored in Re average, Figure 2.). The relative difference between minimum and 240 maximum lift (d), drag (e), and power factor (f) among wings is substantial (green line, std calibration 241 242 accuracy for reference). The optimal aspect ratio to obtain maximum (red) versus minimum (blue) 243 lift (g), drag (h), and power factor (i) depends on incidence. The color intensity corresponds with the 244 p-value of the Wilcoxon rank-sum test for aspect ratio at constant incidence. The effect of aspect ratio on power factor at  $\alpha = 0^{\circ}$  could not be established due to numerical sensitivity to experimental 245 246 error near zero lift, which produced outliers that were disregarded (vertical black area at  $\alpha = 0^{\circ}$ ).



Figure S5. Reynolds number has limited effect on force coefficients across Re = 9,000-25,000. (a-c) 248 249 Lift, drag and power factor versus angle of attack as a function of aspect ratio. Aspect ratio 4 and 5 250 wings combine near maximal lift, and intermediate drag, which maximizes power factor beyond 20°. 251 A single outlying point for the drag coefficient is marked as a dot. The relative difference between 252 minimum and maximum lift ( $\mathbf{d}$ ), drag ( $\mathbf{e}$ ), and power factor ( $\mathbf{f}$ ) among wings is substantial (green line, 253 std calibration accuracy for reference). The optimal aspect ratio to obtain maximum (red) versus 254 minimum (blue) lift (g), drag (h), and power factor (i) depends on incidence. The color intensity 255 corresponds with the p-value of the Wilcoxon rank-sum test for aspect ratio at constant incidence. Motor power limited the achievable incidence range for aspect ratio 8 and 10 wings at Re = 21,000-256 25,000 (horizontal black areas). The effect of aspect ratio on power factor at  $\alpha = 0^{\circ}$  could not be 257 established due to numerical sensitivity to experimental error near zero lift, which produced outliers 258 259 that were disregarded (vertical black area at  $\alpha = 0^{\circ}$ ).



Figure S6. The leading edge vortex remains attached at radii up to 4 chord lengths at 30°. Average vorticity concentration at Re = 13,000 reveals an attached leading edge vortex inboard of  $r / c \sim 4$ . Outboard vortices detach from the leading (yellow, red) and trailing edge (blue). We masked the vorticity field on the inboard leading edge of the aspect ratio 6.5 wing because stove polish proved unsuccessful to reduce background reflections on the plastic wing mount and carbon fiber hooklet in those particular images. One flow field close to the tip of the aspect ratio 6.5 wing was not recorded at 30° and is therefore not shown.



Figure S7. Reynolds number has limited effect on vorticity around an aspect ratio 4 wing across Re = 5,000-25,000. Average vorticity concentrations are similar for different Re, at both 30° and 45° incidence. A leading edge vortex attached to the inboard wing merges with the tip vortex outboard, as shown for maple seeds <sup>23</sup>.



Figure S8. A non-local vortex detection scheme confirms that the leading edge vortex is either attached to, or tilted away from, the surface as a function of radial position r / c. The vortex identification results are similarly robust for (**a**), the aspect ratio 4 wing with R/c = 4.6 and (**b**), the aspect ratio 10 wing, with R/c = 10.6, at 30° and 45° incidence and Re = 13,000. The thin black contour lines represent a non-local scalar measure for axisymmetric vortex intensity ( $\gamma = 0.4$ and  $\gamma = 0.6$ ), which coincide with the peaks in the average local vorticity field (shown as color intensity in the background). Both the non-local vortex intensity and the local vorticity field show

that the LEV is attached to the wing surface inboard (low r/c), and is detached from the surface outboard (high r/c). We thus conclude that our vorticity fields are sufficiently noise-free to detect vortices based on vorticity concentration. The thick black lines show the model wing cross-section; gray areas mask the area below the wing where the laser illumination was insufficient. The axisymmetric vortex intensity at a point P in the velocity field is defined as  $\gamma(P) = \frac{1}{N} \sum \sin(\theta_M)$ following the work of Graftieaux *et al.*<sup>14</sup>, which was implemented using MATLAB code from Jones *et al.*<sup>13</sup>.





Movie S1 (still). Strong radial differences in LEV dynamics and flow separation are visible along the wing. The movie shows a loop of twenty instantaneous vorticity fields at three spanwise stations on an aspect ratio 10 model wing at 30° and 45° incidence. Inboard, the LEV is attached to the upper wing surface, whereas outboard vortex shedding and strong flow separation reveal the leading edge vortex is unsteady.

## 299 Cited References

- Lentink, D. & Dickinson, M. H. Rotational accelerations stabilize leading edge vortices on revolving fly wings.
   *J Exp Biol* 212, 2705-2719, doi:10.1242/jeb.022269 (2009).
- Hein, B. R. & Chopra, I. Hover performance of a micro air vehicle: rotors at low Reynolds number. *Journal of the American helicopter Society* 52, 254-262 (2007).
- Bohorquez, F., Pines, D. & Samuel, P. D. Small rotor design optimization using blade element momentum
   theory and hover tests. *Journal of aircraft* 47, 268-283 (2010).
- Harbig, R., Sheridan, J. & Thompson, M. Reynolds number and aspect ratio effects on the leading-edge vortex
   for rotating insect wing planforms. *Journal of Fluid Mechanics* 717, 166-192 (2013).
- Altshuler, D. L., Dudley, R. & Ellington, C. P. Aerodynamic forces of revolving hummingbird wings and wing
   *Journal of Zoology* 264, 327-332 (2004).
- Weis-Fogh, T. Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift
   production. *Journal of Experimental Biology* 59, 169-230 (1973).
- 312 7 White, F. M. Viscous Fluid Flow. (McGraw-Hill, 1991).
- 313 8 Usherwood, J. R. & Ellington, C. P. The aerodynamics of revolving wings I. Model hawkmoth wings. *J Exp*314 *Biol* 205, 1547-1564 (2002).
- Usherwood, J. R. & Ellington, C. P. The aerodynamics of revolving wings II. Propeller force coefficients from mayfly to quail. *J Exp Biol* 205, 1565-1576 (2002).
- Wang, Z. J. Aerodynamic efficiency of flapping flight: analysis of a two-stroke model. *Journal of Experimental Biology* 211, 234-238 (2008).
- 319 11 Eilers, P. H. A perfect smoother. *Analytical Chemistry* 75, 3631-3636 (2003).
- Poelma, C., Dickson, W. & Dickinson, M. Time-resolved reconstruction of the full velocity field around a dynamically-scaled flapping wing. *Experiments in Fluids* 41, 213-225 (2006).
- Jones, A., Pitt Ford, C. & Babinsky, H. Three-dimensional effects on sliding and waving wings. *Journal of Aircraft* 48, 633-644 (2011).
- Graftieaux, L., Michard, M. & Grosjean, N. Combining PIV, POD and vortex identification algorithms for the
   study of unsteady turbulent swirling flows. *Measurement Science and Technology* 12, 1422 (2001).
- Unal, M., Lin, J.-C. & Rockwell, D. Force prediction by PIV imaging: a momentum-based approach. *Journal of Fluids and Structures* 11, 965-971 (1997).
- Wu, J.-Z., Pan, Z.-L. & Lu, X.-Y. Unsteady fluid-dynamic force solely in terms of control-surface integral.
   *Physics of Fluids (1994-present)* 17, 098102 (2005).
- 330 17 Dabiri, J. O. On the estimation of swimming and flying forces from wake measurements. *Journal of Experimental Biology* 208, 3519-3532 (2005).
- 332 18 Van Oudheusden, B., Scarano, F. & Casimiri, E. Non-intrusive load characterization of an airfoil using PIV.
   333 *Experiments in fluids* 40, 988-992 (2006).
- Wu, J.-Z., Lu, X.-Y. & Zhuang, L.-X. Integral force acting on a body due to local flow structures. *Journal of Fluid Mechanics* 576, 265-286 (2007).
- 336 20 Spedding, G. R. & Hedenström, A. PIV-based investigations of animal flight. *Experiments in Fluids* 46, 749-763
   337 (2009).
- 338 21 Van Oudheusden, B. PIV-based pressure measurement. *Measurement Science and Technology* 24, 032001 (2013).
- 340 22 Mohebbian, A. & Rival, D. E. Assessment of the derivative-moment transformation method for unsteady-load
   341 estimation. *Experiments in fluids* 53, 319-330 (2012).
- Lentink, D., Dickson, W. B., van Leeuwen, J. L. & Dickinson, M. H. Leading-Edge Vortices Elevate Lift of
   Autorotating Plant Seeds. *Science* 324, 1438-1440, doi:10.1126/science.1174196 (2009).
- 344 345