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Aerodynamic explanation of flight speed limits in hawkmoth-like flapping-wing insects

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ABSTRACT

The hawkmoth is able to sustain a steady hover or level flight at lower speeds. However, previous wind tunnel experiments have suggested that long sequences of steady forward flight are less common at higher flying speeds (>4.0 m/s) despite changes to the flight posture. This flying speed is about one-half of the theoretical prediction based on its body mass. It is unclear why hawkmoths have not been observed achieving steady flight at higher speeds. This study aims to compare the aerodynamics involved in hawkmoth hovering to those in forward flight. High-speed video recordings and 3D surface reconstruction were used to capture a hawkmoth's wing kinematics when hovering and at forward flight speeds of 2 m/s and 4 m/s. Following reconstruction, the insect model was simulated using an in-house immersed-boundary-method based computational fluid dynamics (CFD) solver. The CFD solver provided a quantitative measure of the force generation, power consumption, and vortex structures generated during sustained flight. These results enabled the analysis of certain trends in how a hawkmoth adjusts flapping kinematics and its associated unsteady aerodynamics changes across different flight speeds. The results show that the moth minimizes drag as flying speed increases, but it immediately loses its lift producing upstroke even at the slow forward flight speed (2 m/s). A significant amount of negative lift is generated during upstrokes at the high forward flying speed (4 m/s). This negative lift in the upstroke potentially reduces maximum sustained flight speeds. This work provides physical insight into the low-speed flights in flying insects.

Key words: flapping wings, unsteady aerodynamics, vortex dynamics

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1 Introduction

As insects flap their wings, they create tornado-shaped leading-edge vortex (LEV) above the wing surface to generate sufficient aerodynamic force required to perform various flight tasks [1]. As a consequence, the unsteady flow evolves to a trail of aerodynamic footprints (complex vortex structures) in the wake. Among all flight modes, the two most widely studied modes are hovering and forward flight due to their potential broader applications in man-made robotic designs. In order to achieve a sustained flight mode at a fixed position (hovering) or at a constant forward flight speed (cruising), insects need to adjust their wing movements to reach a force balance in both vertical and horizontal directions.

Previous studies have used several different methods to examine how insects' kinematics and aerodynamics change as their flight speed increases. Dudley & Ellington [2, 3] used high-speed cinematography and a force transducer to measure bumblebee wing kinematics and aerodynamic performance over a range of flight speeds (0 m/s-4.5 m/s). They found that as a bumblebee's forward flying speed increases, its wing angle of attack relative to the stroke plane also increases. In addition, during hovering flight, the bumblebee's downstroke and upstroke were shown to provide equal contributions to its total lift. However, as the bumblebee transitions to forward flight, its downstroke plays an increasingly dominant role in lift production. Zhu & Sun [4] demonstrated a similar trend using computational fluid dynamics (CFD) simulations of fruit fly forward flight. Results showed that as a fruit fly's flight speed increases, its stroke plane becomes more vertical, and its wing angle of attack during the upstroke increases. In addition, a fruit fly's downstroke contributes approximately half of the total lift at low forward flying speeds, while at high forward flying speeds, the downstroke contributes almost all of the total lift. Song et al. [5, 6] also performed CFD simulations of hummingbird hovering and fast forward flight. Results showed that during hummingbird hovering, lift production is asymmetric between the downstroke and upstroke, with the downstroke producing 74% of the total lift, consistent with particle imaging velocimetry results [7]. During hummingbird fast forward flight, the downstroke contributes all of the total lift, and negative lift is generated during the upstroke. Song et al. suggest that at high hummingbird forward flying speeds, the upstroke is used to generate thrust at the cost of lift production. In a separate study, Suzuki et al. [8] simulated forward flight of a butterfly-like flapping model with various flapping kinematics and Reynolds numbers. Their parametric study demonstrated most of the lift force was generated during the downstroke. The backward flapping motion during the upstroke created a significant negative lift force, and the magnitude of the negative lift could be modified by tuning the maximum angle of attack of flapping cycle.

The hawkmoth (*Manduca sexta*) is another small flying animal capable of both hovering and forward flight. Hedrick & Daniel [9] discovered many different sets of kinematic parameters capable of producing hovering flight in a model hawkmoth. Their results suggest that the flapping mechanism used in hawkmoth flight is likely determined by factors beyond kinematic and aerodynamic performance. These

factors may include biological constraints, such as the ability to apply a single wingbeat pattern to several different flight modes. For a flying animal of its size, a hawkmoth's maximum forward flying speed has been reported much lower than expected. Stevenson et al. [10] used the hawkmoth's body mass to calculate a theoretical maximum flying speed of 7-10 m/s. However, experimental results have shown that hawkmoths are incapable of sustaining steady forward flight at speeds greater than 5m/s [11, 12]. Studying how a hawkmoth's wing kinematics and aerodynamics change as its flight speed increases can help explain why its maximum forward flying speed is lower compared to other flying animals with similar body mass, such as hummingbirds. Willmott & Ellington [11] used high-speed videography to calculate a hawkmoth's wing kinematics for flight speeds ranging from 0 m/s (hovering) to 5 m/s (forward flight). Results showed that as the hawkmoth's flying speed increased, its stroke plane angle became more vertical. This trend is consistent with the previously discussed results for other flying animals. Willmott & Ellington [13] also studied the aerodynamic performance of hawkmoths flying over the same range of speeds. They used a modified blade-element (BEM) approach to calculate the mean lift and drag coefficients for stationary hawkmoth wings. Because the wings were stationary, a time history of the instantaneous lift and drag was not provided. In addition, the researchers were able to qualitatively determine that the downstroke increasingly dominates lift support as forward flying speed increases, but exact contributions were not calculated in their study.

In addition to the above experimental measurements, Aono et al. [14] used real insect data to perform CFD simulations of hawkmoth hovering. The researchers noted the formation of a doughnut-shaped vortex ring in the wake of the hovering hawkmoth. Their results showed that the downstroke and upstroke both provided significant contributions to the total lift, but simulations for hawkmoth forward flight were not part of this study. Zheng et al. [15] also used real hawkmoth hovering data to compare CFD simulation results with a BEM based approach. Results showed that the BEM approach did not match the predictive abilities of the CFD. The researchers also found that for hawkmoth hovering, most of the lift is generated during the downstroke, similar to results from hummingbirds. This study also did not include any simulations of hawkmoth forward flight. Yao & Yeo [16] performed CFD simulations of both hawkmoth hovering and forward flight. However, wing kinematics were prescribed using a generic proportional-integral-derivative (PID) controller and were not based on real hawkmoth flapping data. Results from this study showed that for hawkmoth hovering, the downstroke and upstroke provided approximately equal contributions to the total lift generated during each wingbeat. At a forward flying speed of 1.3 m/s, the downstroke provided most of the lift, but positive lift was still generated during the upstroke. At all flight speeds greater than 1.3 m/s, the upstroke generated negative lift. Yao & Yeo suggest that this trend is due to the highly vertical stroke plane at high forward flying speeds.

As described above, prior experimental measurements and computational simulations of hawkmoth flight have mainly focused on hovering. The exception, Yao & Yeo [16], performed CFD simulations of hawkmoth forward flight, but used a flat-plate wing with flapping kinematics prescribed as sinusoidal equations. The present study is among the first to use real hawkmoth flight data to simulate hawkmoth flight over a range of flying speeds. We aim to find out what prevents the hawkmoth from achieving a fast forward flying from a fluid dynamics perspective. In the current study, hawkmoth wing kinematics were reconstructed based on high-speed video recordings of flying hawkmoths at speeds of 0 m/s, 2 m/s, and 4 m/s in a wind tunnel. The reconstructed hawkmoth model was then simulated using an in-house immersed boundary method (IBM) based in-house CFD solver. Simulation results were used to calculate instantaneous lift and drag forces produced by the flying hawkmoth, and power consumptions required to achieve different flight motions. The force generation on the deformable wing surfaces and its associated near and far wake structures were compared across different flying speeds.

2 Methodology

2.1 Experimental setup and filming procedures

Hawkmoths were recorded flying at three different flight speeds- hovering (0 m/s), slow forward flight (2 m/s), and fast forward flight (4 m/s). Moths were males acquired as pupae from the domestic colony in the Department of Biology at the University of North Carolina at Chapel Hill. Following eclosure, moths were placed in individual 30×30×30 cm mesh cages in an environmental chamber maintaining ~25°C and a 20:4 Light/Dark cycle. Before filming, moths were not fed for a minimum of 12 hours. At recording, each moth was placed inside a wind tunnel (octagonal working section, 1.2m long and 0.6m diameter, see Ortega-Jimenez et al. [17] for further details), and an artificial flower with a 1 to 4 honey water mix ratio was provided for the insect to feed on; moths were trained via prior experience to recognize the flower and feed from it at a variety of tunnel flow speeds. Three high-speed cameras (two Phantom v7.1 equipped with 35mm Nikon lenses, and one Phantom v5.1 with a Zeiss 50mm lens, Vision Research Inc., Wayne, NJ, USA) operating at 1000 frames s⁻¹ with a 300 μs shutter duration were used to record hawkmoth flight. Illumination for the cameras was provided by four 12 W multi-LED infrared (730 nm) lights (Larson Electronics LLC, Kemp, TX, USA); these emit at a wavelength below the hawkmoth visual spectrum and thus do not alter flight behavior. The cameras were calibrated for 3D kinematics using a structure-from-motion approach [18]. During the experiments, the flight speed is controlled by changing wind tunnel speeds without removing the animal. Recordings from a single individual flying at different flight speed were selected for detailed 3D reconstruction and meshing for computational simulation. The morphological data for the hawkmoth used in this study is summarized in Table 1. Note that the moth was allowed to hover and feed to satiation after the video data were collected, and the pre-feeding mass from Table 1 is expected

to be characteristic of the moth during recordings. The flight speeds were recorded in the following order:
2 m/s, 4 m/s, and 0 m/s.

Table 1. Morphological data for the hawkmoth in this study. The data for the wing is presenting a single side wing combining both forewing and hindwing.

Parameter	Values
Body mass before feeding (g)	1.45
Body mass after feeding (g)	1.95
Body length (cm)	5.3
Wing mass (g)	0.0382
Wing span length, R (cm)	5.5
Mean wing chord, c (cm)	2.3
Wing area (cm ²)	10.7
Flapping frequency, f (Hz)	27.9 ± 2.4

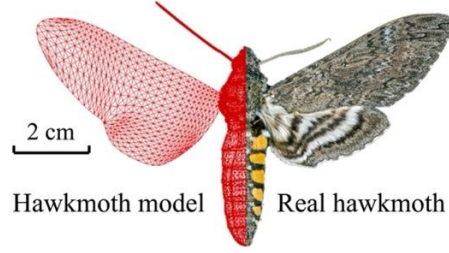


Figure 1. Comparison between hawkmoth meshed model and real hawkmoth. The hawkmoth mesh shown on the left was used for all simulations in this study.

2.2 Reconstruction of hawkmoth flight

After recording hawkmoth hovering (0 m/s), 2 m/s forward flight, and 4 m/s forward flight, a meshed model of the flying hawkmoth was reconstructed using Autodesk Maya. In nature, hawkmoths possess both a forewing and hindwing that combine to provide a lifting surface. However, in this study, we joined the forewing and hindwing into a single mesh to reduce computational complexity. The computational wing used in our simulations is shown on the left in Figure 1. The model hawkmoth was superimposed over the side-view and top-view high-speed video recordings of hawkmoth flight. For each flying speed, one flapping cycle was selected where the hawkmoth body was relatively stationary. At various points throughout the selected wingbeat cycle, the morphology of the model hawkmoth's left wing was adjusted to align with the high-speed recording. The flapping wings of the hawkmoth were reconstructed using a template-based hierarchical subdivision surface method [19, 20]. Using easily identifiable natural patterns on the wing surfaces, we reconstructed the 3D wing kinematics with surface deformation during the flapping wingbeat cycles. During the reconstruction process, we adjusted the subdivision control points to

incorporate these natural twisting/bending deformations. As shown in the high-speed video recordings (included in the supplemental material [21]), the hawkmoth's wings bend and twist considerably during flight. Between these reconstructed points, Fourier interpolation was used to reconstruct hawkmoth flapping motions. A side-by-side comparison between high-speed video recording and reconstructed model is demonstrated in the supplemental material [21].

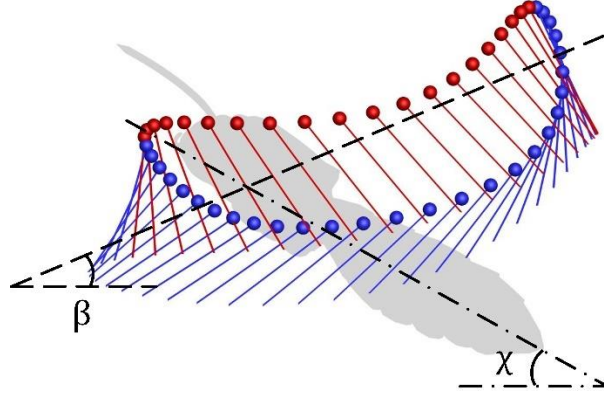


Figure 2. Definition of stroke plane angle (β) and body incline angle (χ). Colored circles in the figure denote the wing leading edge, and the lines present the pitch angle of wing chord at the $0.75R$ along the wingspan. The hawkmoth flapping motion follows a counterclockwise trajectory. The downstroke is pictured in red, and the upstroke is shown in blue. See movie 1 in the supplemental material for reconstructed flapping motions [21].

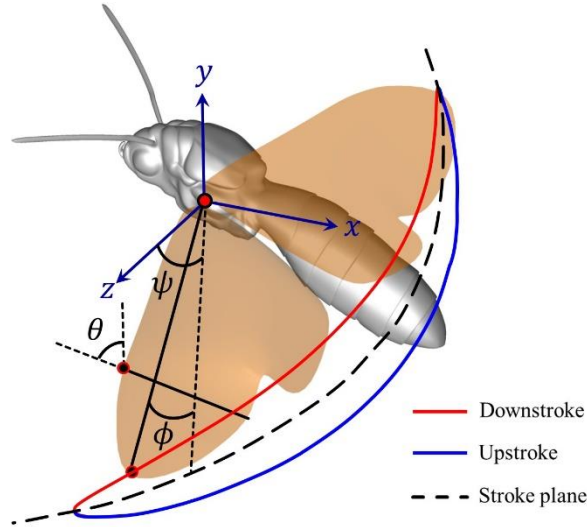


Figure 3. Wing Euler angles definition, including wing stroke (ψ), wing deviation (ϕ), and wing pitch (θ) angles. The wingtip trajectory during the downstroke is shown in red, and the upstroke is shown in blue. Two snapshots of the left hawkmoth wing are shown- one at the beginning of the flapping cycle and one during the downstroke.

Using the reconstructed data, the hawkmoth's body incline angle and stroke plane angle were determined for each flight speed. As shown in Figure 2, the body incline angle is defined as the angle between the hawkmoth body and the horizontal x-axis. The stroke plane angle is defined as the angle between the stroke plane and the x-axis. The stroke plane was determined based on the least square plane of the wingtip trajectory that passes through the wing root and is represented by the dashed line in Figure 3. Next, wing kinematics were quantified on the stroke plane using three Euler angles: wing stroke (ψ), wing deviation (ϕ), and wing pitch (θ). The wing stroke angle provides the location of the wing in the stroke plane, defined as the angle between the projection of the root-to-tip connection line and the z-axis. The deviation angle is the angle between the line from wing root to tip and its projection onto the stroke plane. The wing pitch angle provides the angle between the wing chord and the stroke plane.

2.3 Governing equations and numerical method

The numerical methodology of the immersed-boundary-method-based in-house CFD solver employed in the current study is briefly introduced here. The 3D viscous, incompressible Navier-Stokes equations can be written in a tensor form as follows:

$$\frac{\partial u_i}{\partial x_i} = 0; \quad \frac{\partial u_i}{\partial t} + \frac{\partial (u_i u_j)}{\partial x_j} = -\frac{\partial p}{\partial x_i} + \frac{1}{Re} \frac{\partial}{\partial x_j} \left(\frac{\partial u_i}{\partial x_j} \right) \quad (1)$$

Where u_i are the velocity components, p is the pressure, and Re is the Reynolds number.

The above equations are discretized using a cell-centered, collocated arrangement of the primitive variables, and are solved using a finite difference-based Cartesian grid immersed-boundary method [22]. The equations are integrated in time using the fractional step method. A second-order central difference scheme is employed in space discretization. The Eulerian form of the Navier-Stokes equations is discretized on a Cartesian mesh and boundary conditions on the immersed boundary are imposed through a ghost-cell procedure. Compared to the boundary-conforming methods, such as the curvilinear grid [23-25] and the finite-element methods [26-28], the IBM approach eliminates the need for complicated re-meshing algorithms. It thus significantly reduces the computational cost associated with simulating flow past complex moving boundaries. Immersed boundary methods can be broadly characterized under two categories: continuous forcing approach [29-31] and discrete forcing approach [32-34]. The present study employs a multi-dimensional "ghost-cell" methodology to impose the boundary conditions on the immersed boundary [22]. This method can be categorized as a discrete forcing approach wherein forcing is directly incorporated into the discretized Navier-Stokes equations [35]. The movement of the immersed boundaries (hawkmoth wings) were prescribed according to the image-based reconstruction. This method has been

- 1 successfully applied in the simulations of insect flights [36-38] and bio-inspired propulsions [39-42].
- 2 Validations of the current in-house CFD solver can be found in our previous studies [20, 43-45].

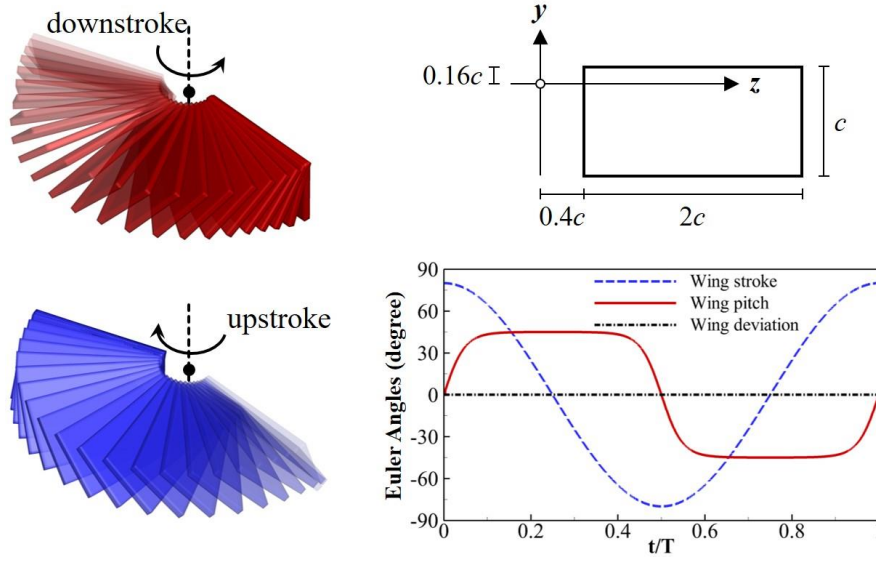


Figure 4. Wing kinematics of a rectangular flapping wing used in solver validation. The benchmark setup is based on Suzuki et al. [8].

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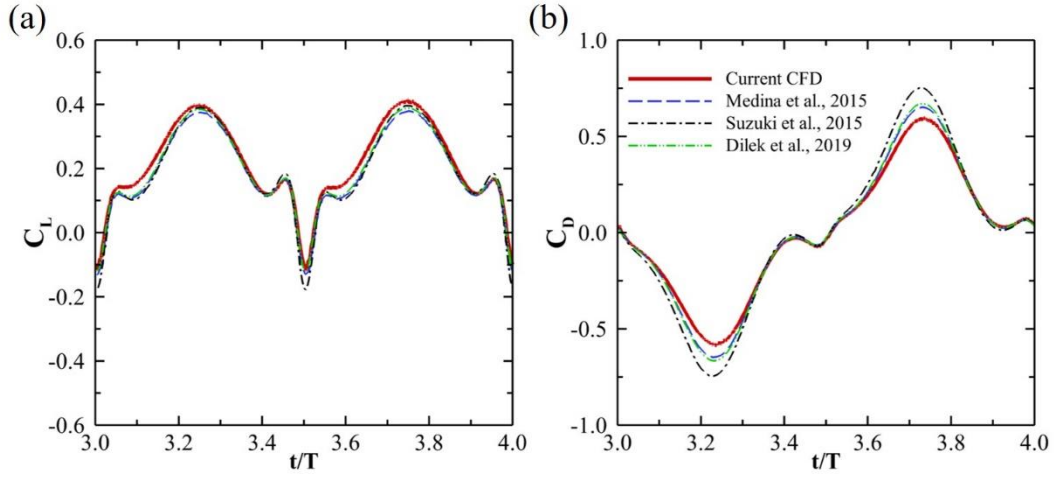


Figure 5. Comparison of lift (a) and drag (b) coefficients of flapping rectangular wing between current CFD results and data available in the literature [8, 46, 47].

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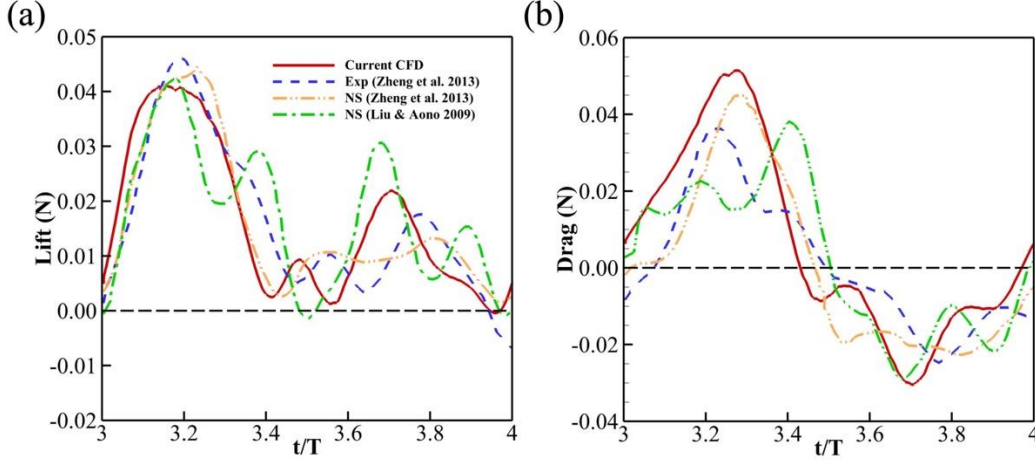


Figure 6. Validation of the in-house CFD solver used in this study. Lift and drag forces produced by a hawkmoth's wings and body in hovering flight are plotted against previous experimentally and computationally determined results. Experimental and numerical results obtained by Zheng et al.[15] and Aono et al.[14] are included.

2.4 Validation of computational modelling

2.4.1 Flapping rectangular wing

To demonstrate the validity of the CFD solver, a benchmark setup proposed by Suzuki et al. [8] is used here. The simulation consists of a rectangular wing flapping along a horizontal stroke plane with zero deviation (Figure 4). The rectangular wing has a chord length c , a spanwise length $L=2c$, and a thickness of $w=0.1c$. The wing kinematics are controlled by two rotational angles: wing stroke and wing pitch. The wing stroke angle provides the location of the wing in the stroke plane and is prescribed by $\psi(t) = \psi_m \cos(2\pi ft)$, where $\psi_m=80^\circ$. For the wing rotation along the stroke plane, the wing root is extended out at a distance $0.4c$ away from the vertical rotational axis. The wing pitch angle is given by $\theta(t) = \theta_m \tanh[C_\eta \sin(2\pi ft)] / \tanh(C_\eta)$, in which $\theta_m=45^\circ$ and $C_\eta=3.3$. The rotational axis of wing pitch is located at a distance $0.16c$ from the wing's leading-edge. The Reynolds number ($Re = \bar{U}_{tip} c / \nu$) is set to 100, in which the average tip velocity is calculated by $\bar{U}_{tip} = 2\pi f \psi_m (L + 0.4c)$. A non-uniform Cartesian grid of size $305 \times 137 \times 177$ is used in a computational domain of size $30c \times 30c \times 30c$ to get domain independence results. The simulation is conducted for four flapping cycles. The lift coefficient is calculated by $C_L = 2F_L / (\rho \bar{U}_{tip}^2 Lc)$, and the drag coefficient is calculated by $C_D = 2F_D / (\rho \bar{U}_{tip}^2 Lc)$. Figure 5 shows the lift and drag coefficients from the fourth cycle together with the simulation results from the literature [8, 46, 47]. As can be seen, our simulation results capture the key features of the instantaneous forces well and present a good agreement with the simulation data from the literature.

2.4.2 Hovering hawkmoth

In addition to flapping rectangular wing, the aerodynamic force production of the hovering hawkmoth was compared to previous studies. A reconstruction of hovering hawkmoth flight was created, and the model was immersed in a non-uniform Cartesian computational grid with size $225 \times 193 \times 225$. Following the simulation, aerodynamic lift and drag production was calculated for both wings and the hawkmoth's body. Figure 6 compares our CFD results with the forces calculated by Zheng et al. [15] using both numerical and experimental approaches. In addition, the numerical results obtained by Aono et al. [14] are also included. As illustrated in Figure 6, the force magnitudes and overall trend of our calculations are consistent with the literature. Specifically, the force predictions from the current study are aligned best with the experimental estimation of aerodynamic forces calculated in Zheng's study [15]. It is worth noting that there is some variation between the different studies presented in Figure 6. The discrepancies can be explained by the fact that different hawkmoths were used in each study. Natural variations in wing shape, body size, and flapping kinematics between different individual hawkmoths can lead to slight differences in force magnitude. Despite these differences, the overall trend of force production in the current study is consistent with previous results. Additional validations of the current in-house solver can be found in our previous studies [20, 36, 40, 43, 45].

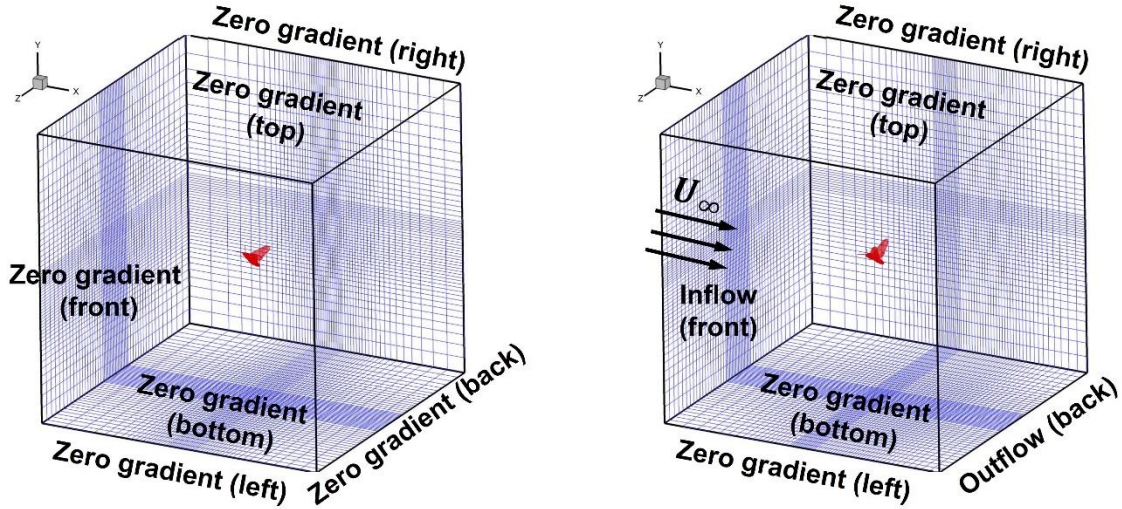


Figure 7. Simulation setup and computational grids applied in the study. Grids are shown for hovering (left) and forward flight (right).

2.5 Simulation setup

Figure 7 shows the simulation setup for both hovering and forward flight. The domain mesh has two refined layers. As seen in this figure, a very high-resolution mesh is provided in a rectangular region around the

hawkmoth. Around this region, there is a secondary denser mesh, and beyond this layer, the grid is stretched rapidly. Different computational grids were used for hovering and forward flight to accommodate different relative positions of downwash. In addition, different boundary conditions were also applied to the two meshes. For hovering, a zero gradient was used for all boundaries. For forward flight, the inflow boundary condition was specified at the front of the fluid domain, while an outflow boundary condition was used at the back of the fluid domain. At all other boundaries, a zero gradient was adopted. The forward flight grid contains approximately 1 million more computational cells than the grid used for hovering flight. In order to achieve a periodic state of the force history, all simulations were run for 4 flapping cycles. We concluded that the force history was periodic after four flapping cycles, because the difference in cycle-averaged lift between the third and fourth flapping cycles was very small ($< 2\%$ for all three flight conditions). The simulation results we present in the results section are based on the 4th flapping cycle.

The simulations were carried out on a non-uniform Cartesian grid. The grid size employed in the current simulations is $225 \times 193 \times 225$ ($\Delta x \cong 0.0044R$) for hovering and $313 \times 153 \times 225$ ($\Delta x \cong 0.0041R$) for forward flight. To ensure the simulation results are grid-independent, grid independence studies were performed for both hovering flight and forward flight at 4 m/s. Figure 8 shows the comparison of simulated lift and drag for a single hawkmoth wing in three grids of different densities at hovering. The coarse mesh presents slightly higher peak values for both lift and drag forces compared to other two meshes. This can partly be explained by the pressure oscillation of the immersed-boundary method when the mesh resolution is not sufficient for the moving boundaries. When the medium mesh is applied for the simulation, the difference between the cycle average force for the medium and fine meshes is less than 3% for both lift and drag, which indicates that grid-independent results are achieved.

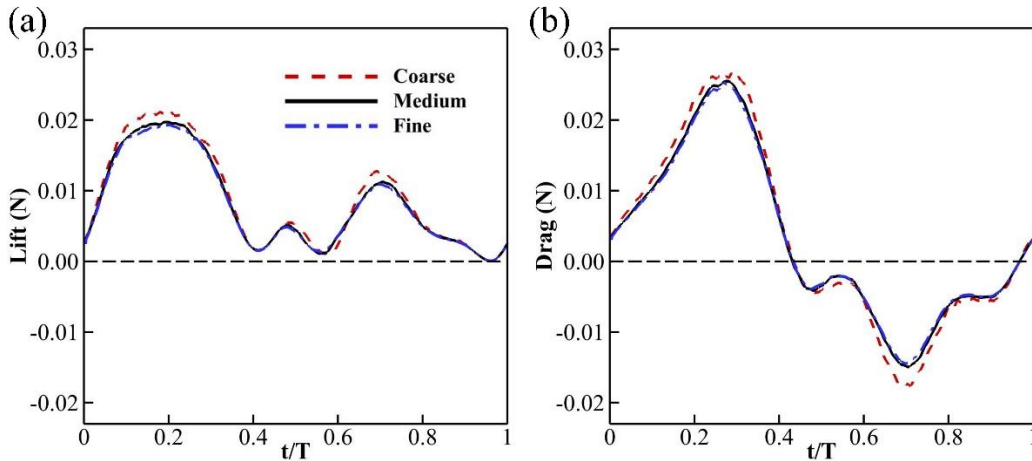


Figure 8. Lift and drag force production during hovering flight by a single hawkmoth wing. Results are shown for three different grid densities: coarse ($177 \times 145 \times 177 \approx 5$ million, $\Delta x \cong 0.0096R$), medium ($225 \times 193 \times 225 \approx 10$ million, $\Delta x \cong 0.0044R$), and fine ($257 \times 225 \times 257 \approx 15$ million, $\Delta x \cong 0.0019R$).

In the present study, we observed that the hawkmoth slightly changed its flapping frequency as the flying speed increased from 0 m/s (hovering) to 4 m/s (forward flight). In order to make a fair comparison, we incorporate both cycle-averaged wing-tip velocity and flight speed in the definition of Reynolds number. Following the previous literature [48], the Reynolds number (Re) and advance ratio (J) in our study are defined as:

$$Re = \frac{(\bar{U}_{tip} + U_{\infty})c}{\nu} = \frac{(1+J)(2\Phi fR)c}{\nu} \quad (2)$$

$$J = \frac{U_{\infty}}{\bar{U}_{tip}} = \frac{U_{\infty}}{2\Phi fR} \quad (3)$$

Where U_{∞} represents the body moving velocity (zero for the hovering case); $\bar{U}_{tip}$ is the mean wing tip velocity and can be expressed as $2\Phi fR$, in which Φ is the stroke amplitude, f is the flapping frequency, and R is the wing root to tip length (0.055m for all cases); c is the average wing chord length (0.023m for all cases); and ν is the fluid kinematic viscosity (around $1.56 \times 10^{-5} \text{ m}^2\text{s}^{-1}$ for air at room temperature of 25°C).

2.6 Evaluation of power consumption

In this study, the mechanical power (P_{mech}) was calculated using a similar treatment as presented by Wan et al. [49] and Aono & Liu [50]. The mechanical power includes two components, namely, aerodynamic power (P_{aero}) and inertial power (P_{iner}). Specifically, the aerodynamic power is the power needed to overcome air resistance, and it is defined as the scalar products of the velocity and the aerodynamic force of the wing (Eq. 4).

$$P_{aero} = - \sum_i^N (F_{aero,i} \cdot v_i) \quad (4)$$

$$P_{iner} = \iint \bar{\rho}_w \bar{h} \frac{d\mathbf{u}_c}{dt} \cdot \mathbf{u}_c ds \quad (5)$$

The inertial power is the power needed to accelerate each wing, and it is defined as the surface integral of the product of the average wing density, average wing thickness, acceleration of each element, and the velocity of each element (Eq. 5). In our calculation, the product $\bar{\rho}_w \bar{h}$ was calculated as the wing mass divided by the wing surface area (m_{wing}/S). The mechanical power required to move each wing is the sum of the aerodynamic power and the inertial power (Eq. 6). The power can be normalized by dividing by the body mass (m_b) of the hawkmoth to compute the mass-specific power (Eq. 7).

$$P_{mech} = P_{aero} + P_{iner} \quad (6)$$

$$P^* = \frac{P_{mech}}{m_b} \quad (7)$$

The true cycle-averaged mechanical power $\bar{P}^*$ depends on the elastic energy storage of the hawkmoth wings and therefore cannot be reported directly. Instead, limiting cases representing 0% and 100% elastic storage must be considered, and the real $\bar{P}^*$ lies between these values [51]. In the case of 0% elastic storage, all negative power is dissipated, and the cycle-averaged mechanical power can be written as

$$\bar{P}_{mech,0\%}^* = \bar{P}^+ \quad (8)$$

In the case of 100% elastic storage, all negative power is stored for later use, and the cycle-averaged mechanical power can be written as

$$\bar{P}_{mech,100\%}^* = \bar{P}^+ - |\bar{P}^-| \quad (9)$$

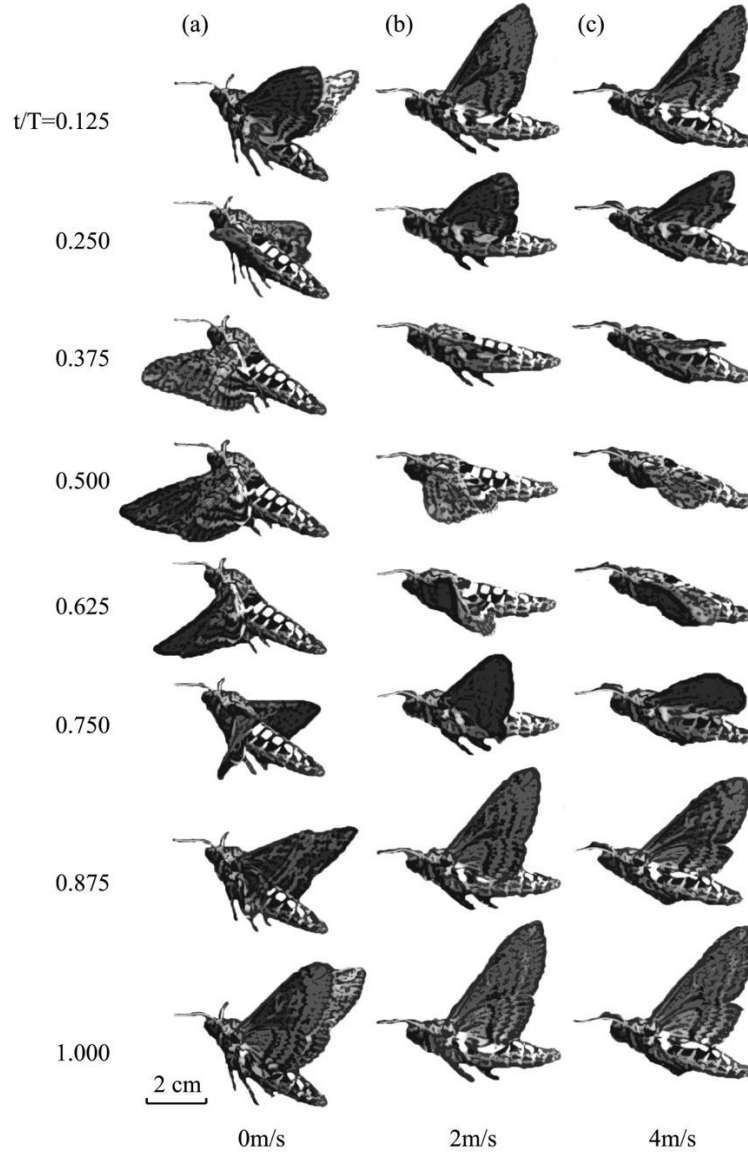


Figure 9. Images of the hawkmoth while (a) hovering and at forward flight speeds of (b) 2 m/s and (c) 4 m/s. See movie 1 in the supplemental material for high-speed video recording [21].

3 Results and discussion

3.1 Flight kinematics at different flying motions

Figure 9 shows image sequences we collected in the experiments for the hawkmoth under hovering motion, 2 m/s forward flight, and 4 m/s forward flight over the course of one wingbeat cycle. Based on these images, it is clear that the hawkmoth's flight kinematics change substantially as the insect transitions from hovering to forward flight. During the hovering downstroke (approx. $t/T=0.125$ to 0.5), the wings sweep horizontally past the body lateral center towards the front of the moth. This 'back-and-forth' flapping behavior indicates a significant negative stroke angle as the hawkmoth begins the upstroke ($t/T=0.5$), as defined in Figure 3. At forward flying speeds, the hawkmoth transitions to a more 'up-and-down' flapping motion. At 4 m/s forward flight, the wings do not reach to the body lateral center at all, resulting in a consistently positive stroke angle. In addition, during hovering flight, the hawkmoth's wings exhibit a significant pitching motion, where they rotate to form an angle with respect to the stroke plane, as defined in Figure 3. The wing pitch during hovering flight is most clearly seen at $t/T=0.5$ and 0.625 in Figure 9. At higher flight speeds, however, the wing pitching motion is less pronounced, with the wings remaining more horizontal throughout the flapping cycle. The hawkmoth's body angle also changes as its flight speed increases. At hovering, the body angle is significantly greater than during forward flight. In addition, Figure 9 shows that at each flying speed, the upstroke begins roughly halfway through the flapping cycle. The duration of the upstroke and downstroke was determined by inspecting the high-speed video of the flying hawkmoth (included in the supplemental material [21]). Each half-stroke begins once the wingtip reverses direction at the end of the previous half stroke. For each flight speed, the downstroke comprises approximately 47% of the flapping cycle duration.

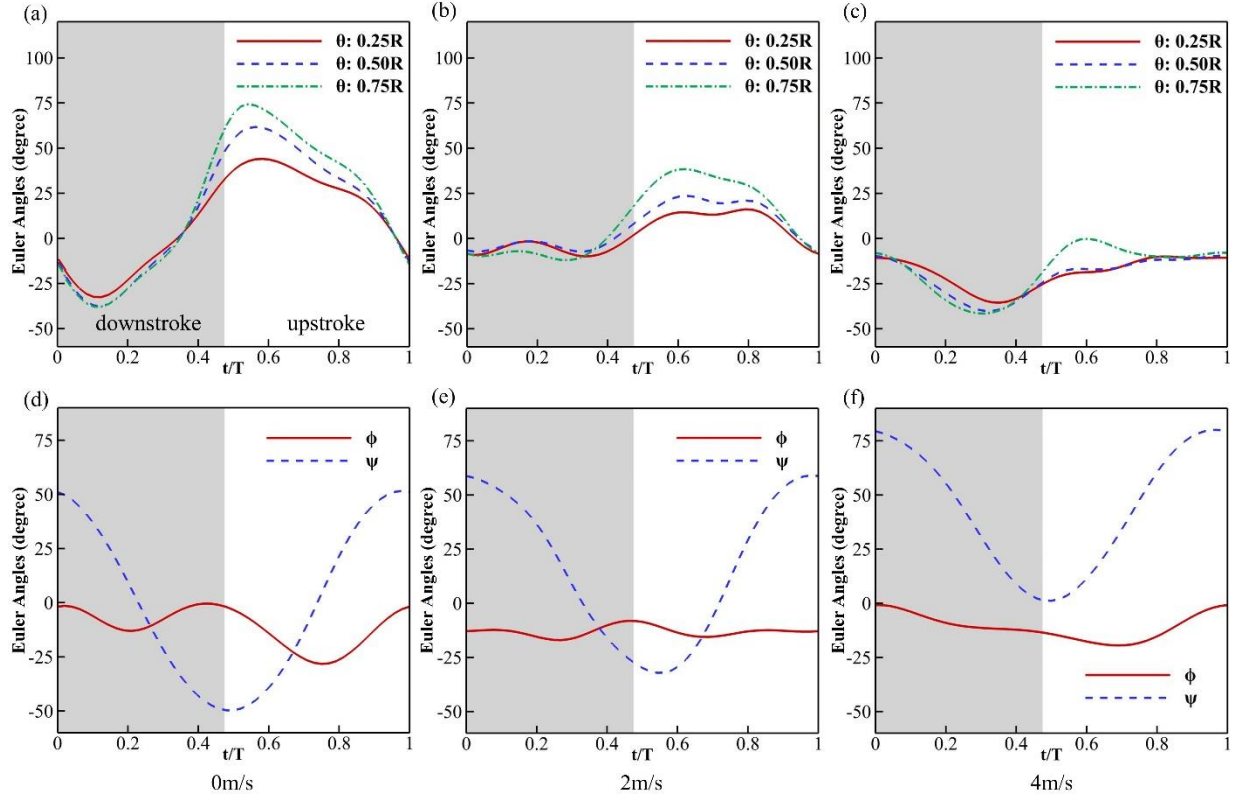


Figure 10. Wing Euler angles for hawkmoth hovering (a, d), 2 m/s forward flight (b, e), and 4 m/s forward flight (c, f). The first row of plots shows the wing pitch (θ) angle at three different locations along the wingspan R . The second row shows the wing stroke (ψ) and wing deviation (ϕ) angles for each flight speed. The downstroke is shaded gray.

For each flight speed, the flapping cycle shown in Figure 9 was used to calculate the wing Euler angles. Figure 10 shows the instantaneous Euler angles during one flapping cycle for hawkmoth hovering, 2 m/s forward flight, and 4 m/s forward flight. The Euler angle plots in Figure 10 reinforce the qualitative observations made using Figure 9. At hovering, the stroke angle ψ ranges from 50° at the beginning of the downstroke to -50° at the beginning of the upstroke. This is evidence of the back-and-forth sweeping flight pattern depicted in Figure 9. At 4 m/s forward flight, the stroke angle is consistently positive. This corresponds to the transition towards a more up-and-down flapping motion at higher flight speeds. Figure 10 also shows that the wing pitch angle tends to peak during the upstroke, and as flying speed increases, the maximum pitching angle decreases. The maximum wing pitch angle at $0.50R$ decreases from 63° at hovering to -10° at 4 m/s forward flight. This is evidence of the decrease in wing pitching motion observed using Figure 9.

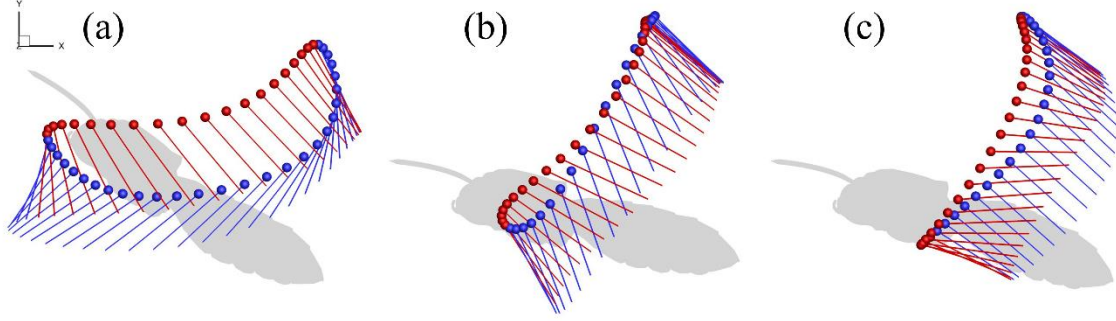


Figure 11. Wing chord trajectory for (a) hawkmoth hovering, (b) 2 m/s forward flight, and (c) 4 m/s forward flight. Colored circles in the figure denote the wing leading edge, and the lines present the wing chord at the 0.75R along the wingspan. The hawkmoth flapping motion follows a counterclockwise trajectory. The downstroke is pictured in red, and the upstroke is shown in blue. See movie 1 in the supplemental material for reconstructed flapping motions [21].

Figure 11 shows the hawkmoth's wing trajectory and wing chord orientation for hovering, 2 m/s forward flight, and 4 m/s forward flight. During hovering flight, the wing chords are significantly more vertical than during 4 m/s forward flight. This is evidence that as the hawkmoth's flight speed increases, its wing pitch angle becomes more parallel to the incoming flow, which potentially reduces the drag force generated during the downstroke. Figure 11 also shows that the stroke plane angle for hawkmoth hovering is smaller than the stroke plane angle for both forward flying speeds. In addition, the body incline angle during hovering flight is greater than during forward flight.

Table 2. Table summarizing significant wing kinematics parameters.

Parameter	Hovering	Slow Forward Flight	Fast Forward Flight
Avg. body moving velocity (U_∞)	0 m/s	2 m/s	4 m/s
Flapping frequency (f)	25.6 Hz	27.8 Hz	30.3 Hz
Stroke amplitude (Φ)	101.22°	91.09°	81.21°
Advance ratio (J)	0	0.41	0.85
Reynolds number (Re)	7335	10117	12863
Stroke plane angle	57.61°	72.54°	66.44°
Body incline angle	30.0°	14.0°	16.0°

We summarized the changes in significant kinematic parameters in Table 2. Table 2 also includes the advance ratio J and Re for different flight speeds. These calculations rely on the flapping frequency f and the stroke amplitude Φ . The flapping frequency is equal to 25.6 Hz for hovering, and it increases to 27.8 Hz and 30.3 Hz for 2 m/s and 4 m/s forward flight, respectively. The stroke amplitude tends to decrease as flying speed increases. Table 1 also shows that the stroke plane angle for both forward flying speeds is greater than for hovering, but the stroke plane angle for 2 m/s forward flight is slightly greater than the

stroke plane angle for 4m/s forward flight. In addition, the body incline angle for forward flight is significantly smaller than the body angle for hovering, but the body incline angle for 4 m/s forward flight is slightly greater than the incline angle for 2 m/s forward flight.

3.2 Evaluation of unsteady aerodynamics of hawkmoth under various flight speeds

Using the reconstructed body and wing kinematics described in the previous section, the unsteady flow and its associated aerodynamic forces were captured using the in-house CFD solver. In Figure 12, we compare the time history of lift (vertical force) and drag (horizontal force) forces on the hawkmoth body and left wing at different flying motions. The overall trend of lift and drag forces are significantly affected by the flying speed of hawkmoth. During hovering flight (Figure 12 (a)), the hawkmoth produces lift during both downstroke and upstroke, with 72% of the lift being generated during the downstroke. However, as the hawkmoth transitions to forward flight, it loses its lift-producing upstroke. At flying speeds of 2 m/s and 4 m/s, positive lift is only produced during the downstroke, and negative lift is generated during the upstroke. It is also worth noting that the lift force in the hovering case peaks three times throughout the flapping cycle: once during the downstroke, once during the transition from downstroke to upstroke, and once during the upstroke. However, during hawkmoth forward flight, the lift peaks only once at mid-downstroke (Figure 12 (b-c)). For all three cases, the cycle-averaged lift generated by two wings matched reasonably well with the body weight of the hawkmoth (see Table 3). As the hawkmoth switched from hovering to forward flight, its body also generated a small amount of lift due to the wing-body interaction [52], a contribution about one order of magnitude smaller than a single wing. In addition to keeping its body aloft in the air, another challenge for the flying hawkmoth is balancing its drag force along the horizontal direction (Figure 12 (d-f)). Although the cycle-averaged drag force is close to zero for all three cases, its magnitude is significantly different at various flying speeds. During hovering flight, the hawkmoth produces a large amount of positive drag during the downstroke and negative drag (thrust) during the upstroke. As the hawkmoth's flying speed increases, the magnitude of drag production is minimized. At 2 m/s, maximum drag production is 0.012N, roughly half the maximum drag during hovering. At 4 m/s forward flight, the drag force production during both downstroke and upstroke is almost negligible. We suspect that minimizing the drag force during the entire flapping cycle is critical to achieving stable fast forward flight for the hawkmoth. By modulating its flapping kinematics to achieve this, the hawkmoth inevitably produces a large amount of negative lift during the upstroke. This biological limitation prevents the hawkmoth from reaching higher forward flying speeds as predicted based on its body size [10].

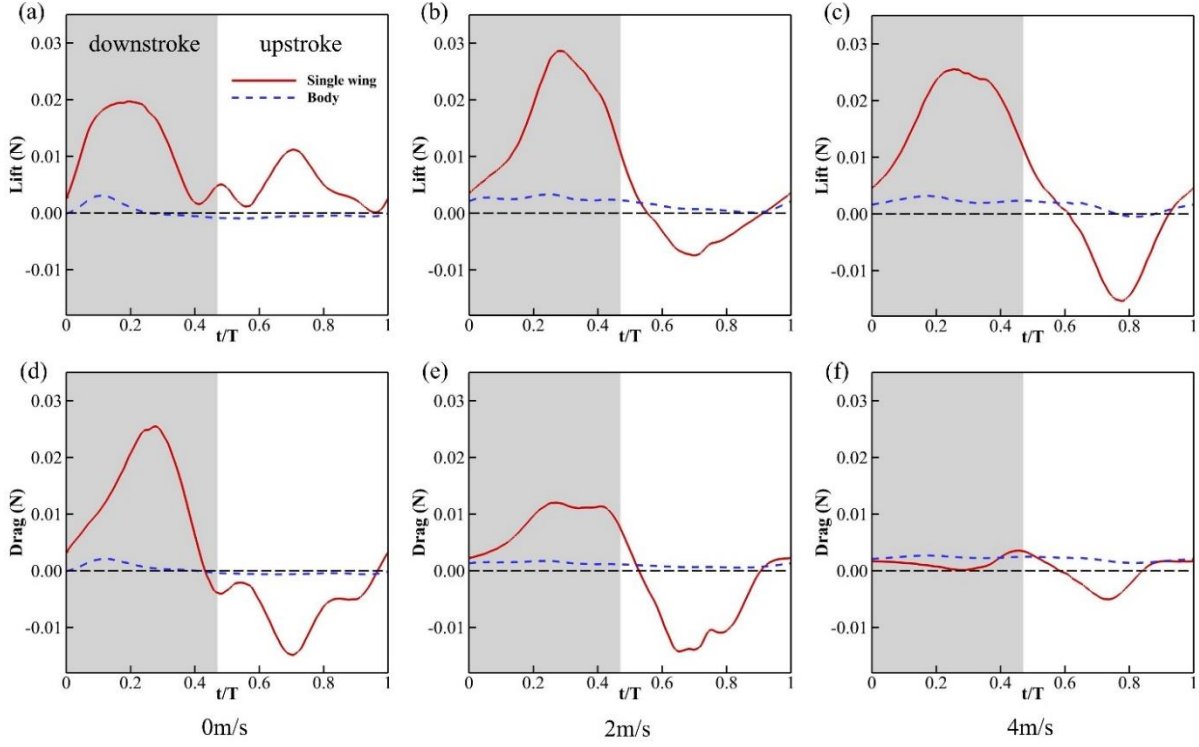


Figure 12. (a-c) Lift and (d-f) drag force production for hawkmoth hovering, 2 m/s forward flight, and 4 m/s forward flight. Force production is shown separately for a single hawkmoth wing and the hawkmoth body. The downstroke is shaded gray.

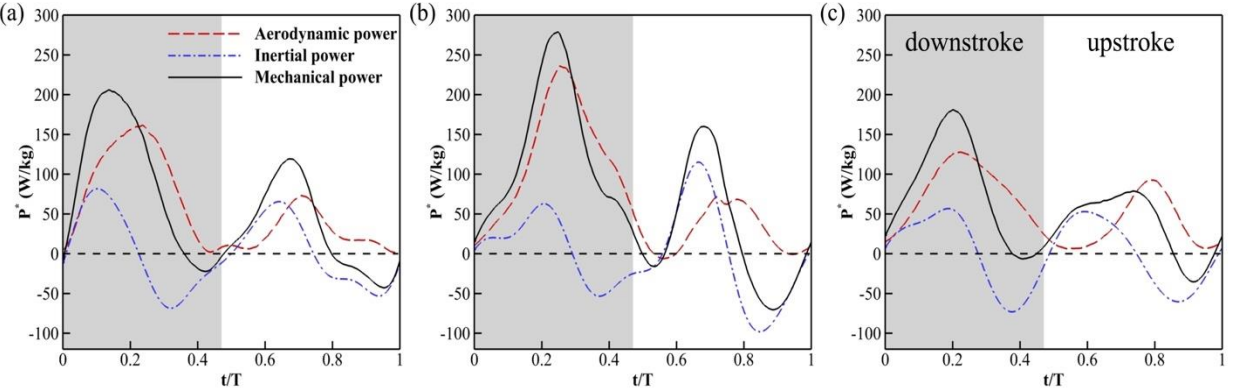


Figure 13. Instantaneous mass-specific aerodynamic, inertial, and mechanical power of wing pair for (a) hovering, (b) 2 m/s forward flight, and (c) 4 m/s forward flight. The downstroke is shaded gray.

One may speculate that the flying speed limitation of hawkmoth observed in nature might be due to the high power consumption in fast flight. In order to evaluate this possibility, we calculated the instantaneous mass-specific aerodynamic, inertial, and mechanical power for hawkmoth hovering, 2 m/s forward flight, and 4 m/s forward flight, as shown in Figure 13. This figure shows that for all flight speeds, the hawkmoth consumes more aerodynamic and mechanical power during the downstroke than during the

upstroke. This is consistent with results previously obtained for other insects [49, 51]. Greater power consumption during the downstroke is likely due to the downstroke's dominant role in lift production. Across all three flying speeds, most of the hawkmoth's lift is generated during the downstroke, resulting in greater power consumption. In addition, Figure 13 shows that the inertial power is positive at the beginning of each half-stroke and negative towards the end of each half-stroke. As a result, the mechanical power briefly becomes negative before each stroke reversal. This may be evidence that the hawkmoth elastically stores some negative power before beginning each stroke. Similar results were obtained by Wan et al. for the cicada [49]. Table 3 reports the cycle-averaged force and power for each flight speed. Since the hawkmoth was feeding occasionally during the recordings, the cycle-averaged lift presents a slight difference between different flight motions. According to our experimental measurements, the body weight of the hawkmoth was 14.2 mN before the recording, and 19.1 mN after all experiments. Table 3 also shows that the cycle-averaged mechanical power for hovering and 2 m/s forward flight is greater than for 4 m/s forward flight. This can be explained by the reduction in drag from the wings as the hawkmoth's flying speed increases (see Figure 12 (e-f)). During 4 m/s forward flight, the hawkmoth produces less drag than it does during hovering and 2 m/s forward flight, and as a result, its cycle-averaged mechanical power is lower. In addition, our results also shed the insights that the speed limit in hawkmoth forward flying seems not directly related to the high power consumption in high-speed flight. This is consistent with a recent particle image velocimetry study of hawkmoth forward flight [53], which also found at the power requirements of flight at the maximum sustained wind tunnel flight speed was less than that of hovering flight.

Table 3. Cycle-averaged lift, mechanical power (with 100% elastic storage), lift-to-power ratio, mass-specific aerodynamic power ($\bar{P}_{aero}^*$), inertial power ($\bar{P}_{iner}^*$), 100% elastic mechanical power ($\bar{P}_{mech,100\%}^*$), and 0% elastic mechanical power ($\bar{P}_{mech,0\%}^*$) for hovering (0 m/s), slow forward flight (2 m/s), and fast forward flight (4 m/s).

Cycle-averaged Values	Hovering	Slow Forward Flight	Fast Forward Flight
Lift (mN)	16.38	16.09	15.22
Mechanical Power (mW)	89.45	90.13	81.50
Lift-to-Power Ratio (N/W)	0.18	0.18	0.19
$\bar{P}_{aero}^*$ (W/kg)	51.32	52.87	47.57
$\bar{P}_{iner}^*$ (W/kg)	1.29	0.15	0.37
$\bar{P}_{mech,100\%}^*$ (W/kg)	52.61	53.02	47.94
$\bar{P}_{mech,0\%}^*$ (W/kg)	87.86	81.06	62.83

Next, we compare the vortex structures generated by hawkmoth across three different flight speeds in Figure 14. Five slides cut along the wingspan demonstrate how the different flapping kinematics modulate the LEV at various flight motions. During hovering flight, a strong LEV is formed and attached

well on the wing surface during both the downstroke and upstroke. At both forward flying speeds, a larger LEV is present during the downstroke (e.g. at $t/T=0.25$ in Figure 14), while a smaller LEV is present during the upstroke (e.g. at $t/T=0.75$ in Figure 14). To take a closer look at LEV formation with different flight motions, we present both three-dimensional and two-dimensional views of slice cuts at the mid-downstroke (Figure 15) and mid-upstroke (Figure 16).

Figure 15 depicts the vortex structures at $t/T=0.25$, and it includes vectors to show the direction of net force at different forward flying speeds during the hawkmoth's downstroke. This figure shows that as the hawkmoth's flight speed increases, the net force vector during the downstroke becomes increasingly vertical. As a result, the drag produced during the downstroke is minimized, as shown graphically in Figure 12 (f). We hypothesize that this minimization of drag may be attributed to flight stability requirements at higher forward flying speeds. The instantaneous momentum at higher flying speed is much higher than that at lower speed. So, the hawkmoth not only needs to maintain a cycle-averaged force balance in the horizontal direction, but also has to minimize the magnitude of drag force oscillation during each stroke. At higher flight speeds, the hawkmoth must limit instantaneous drag force magnitude during its downstroke to keep itself from blowing away in the incoming flow. In order to do so, the hawkmoth must keep its wing pitching angle roughly parallel to the incoming flow when flying at higher forward flight speeds, as seen in Figure 11(c).

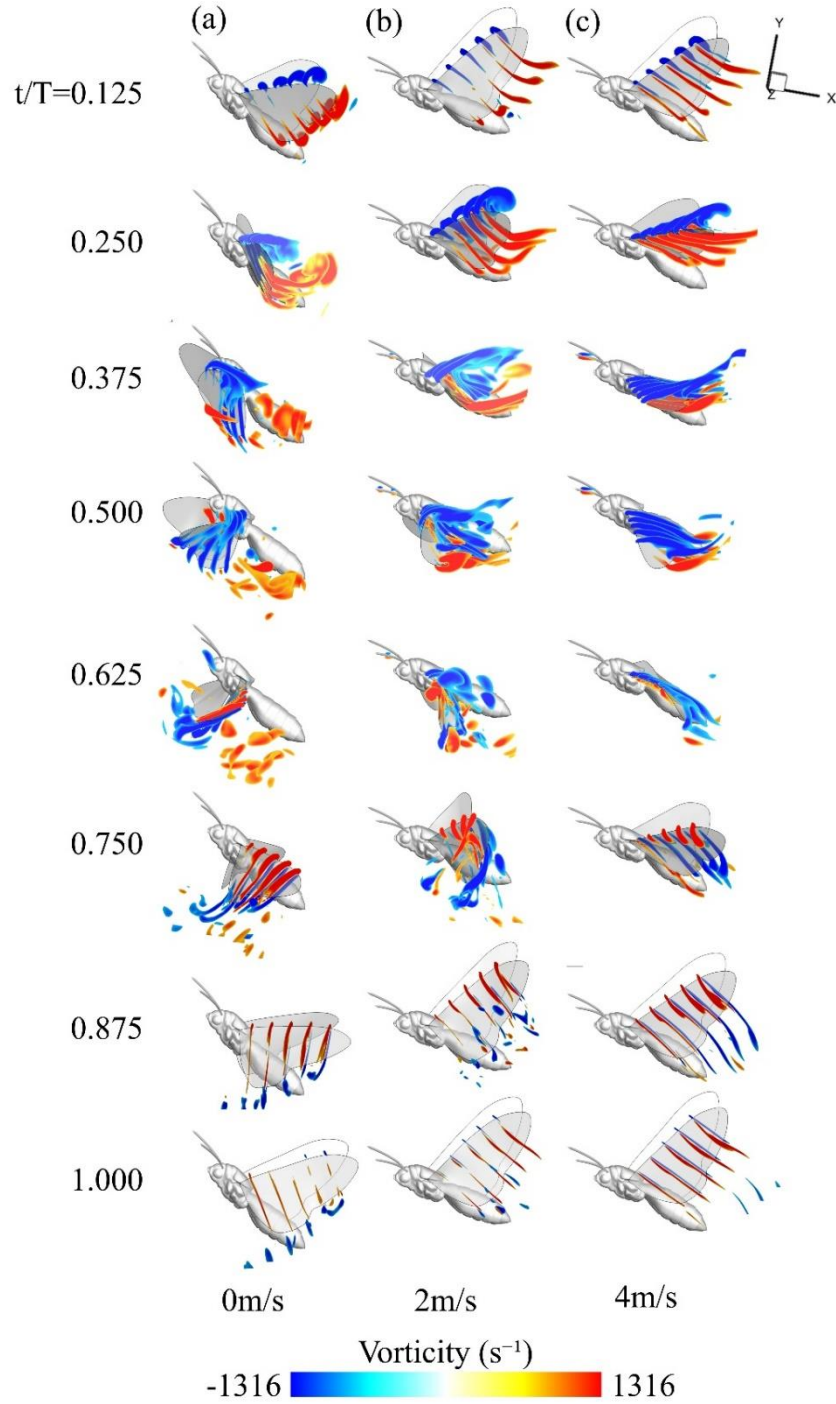


Figure 14. Wing slices throughout one wingbeat cycle for (a) hawkmoth hovering, (b) 2 m/s forward flight, and (c) 4 m/s forward flight. A total of five slices were taken at 0.11R, 0.28R, 0.44R, 0.60R, and 0.77R.

Figure 16 shows the mid-upstroke vortex structures and net force vectors for hovering 2 m/s forward flight, and 4 m/s forward flight. During the hovering upstroke, the wing pitch angle is more vertical,

and the net force is angled upward. During the forward flight upstroke, however, the wing pitch angle is more horizontal, and the net force vector is angled down. As a result, lift is generated during the hovering upstroke but not during the forward flight upstroke, as shown graphically in Figure 12 (a-c). We hypothesize that due to biological limitations, a hawkmoth cannot drastically alter its wing kinematics as it transitions from downstroke to upstroke. As a result, the horizontal wing orientation observed during a forward flying hawkmoth's downstroke is also present during its upstroke. This may explain why the hawkmoth's upstroke is used to generate positive lift during hovering flight but a significant amount of negative lift force generation was observed during 2 m/s and 4 m/s forward flight.

Among all three simulations, we observed two separate LEV above the hawkmoth wing at 2 m/s forward flight, as shown in Figure 17. This phenomenon is also known as a dual LEV and has been observed throughout 1 m/s and 2 m/s hawkmoth flight by Johansson et al.[54]. For the current study, the dual LEV was only visible during the upstroke for the 2 m/s forward flying hawkmoth, but not for the 4 m/s case.

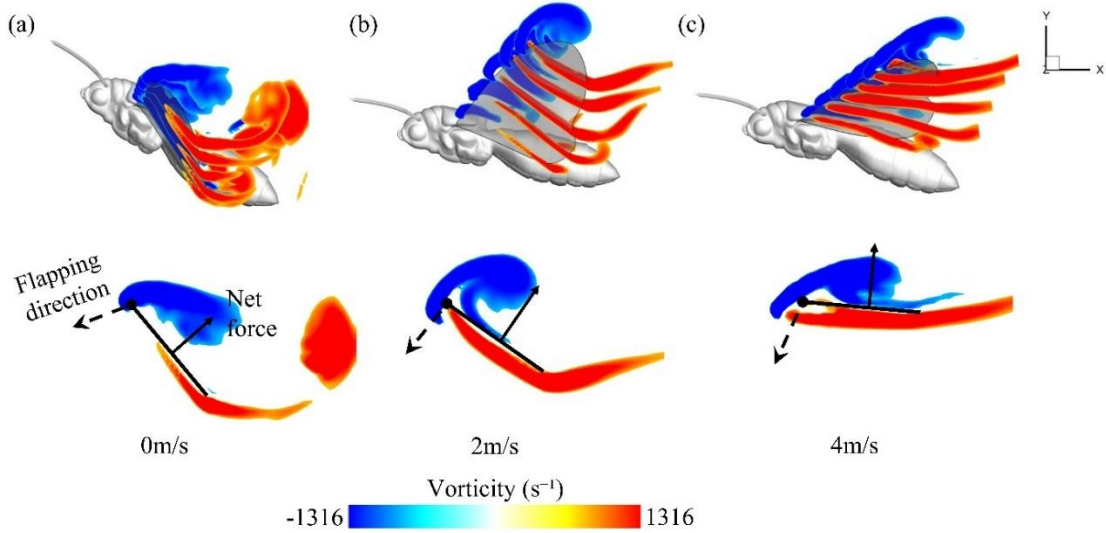


Figure 15. Three-dimensional and two-dimensional views of slice cut vortex structures at mid-downstroke ($t/T=0.25$) for (a) hawkmoth hovering, (b) 2 m/s forward flight, and (c) 4 m/s forward flight. The 2D view is shown for the chord located at $0.60R$. Net force vectors and arrows representing flapping direction are also included. The black circle is located along the wing's leading edge.

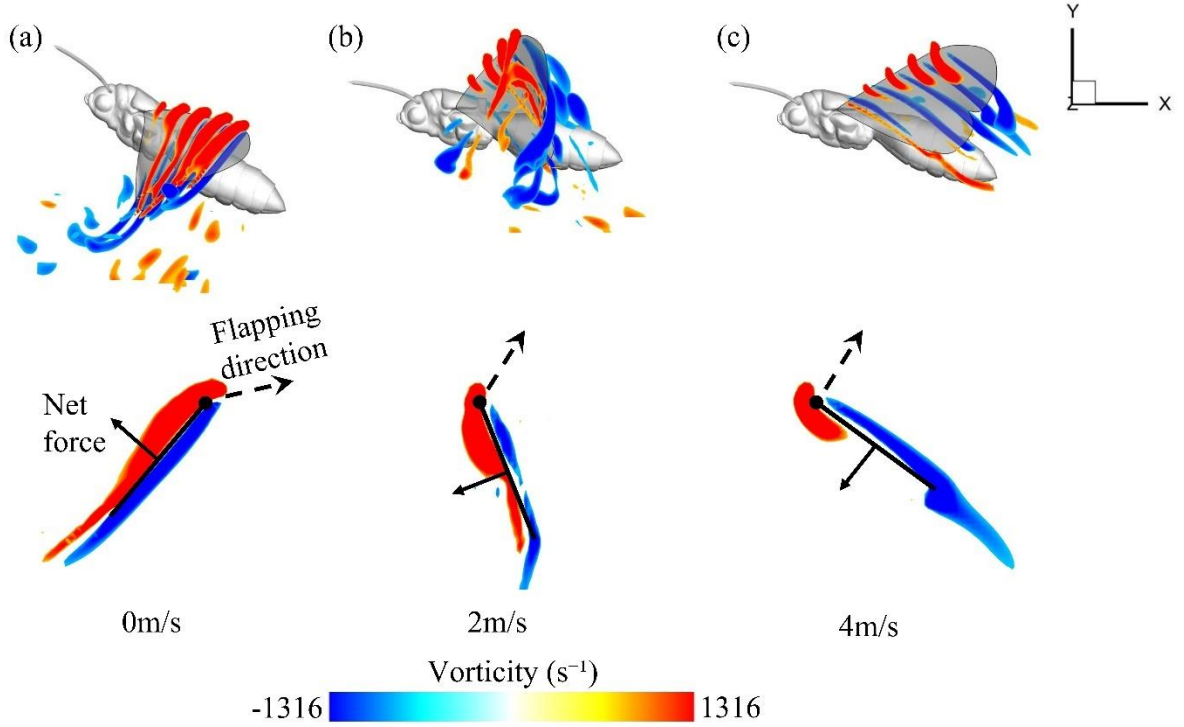


Figure 16. Three-dimensional and two-dimensional views of slice cut vortex structures at mid-upstroke ($t/T=0.75$) for (a) hawkmoth hovering, (b) 2 m/s forward flight, and (c) 4 m/s forward flight. The 2D view is shown for the chord located at $0.60R$. Net force vectors and arrows representing flapping direction are also included. The black circle is located along the wing's leading edge.

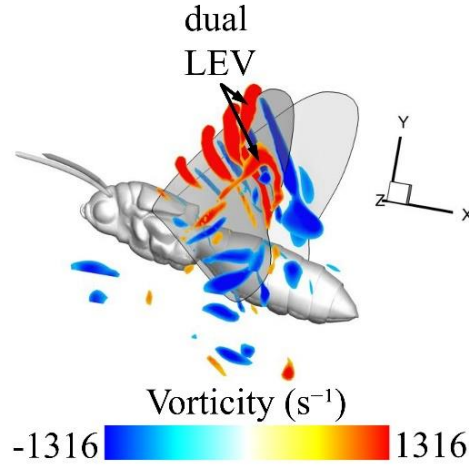


Figure 17. Dual LEV is observed for the hawkmoth forward flight at 2m/s forward flight. The time instant for this picture is at $t/T=0.79$, around the mid-upstroke.

In addition to the visualization of the vortex structures near the wing surface, we also present the far wake structures. Figure 18 shows the time sequence for the flow field at hovering, 2 m/s forward flight,

and 4 m/s forward flight. The vortex structures were plotted using the iso-surface of the Q-criterion. For each flight speed, a strong LEV is formed during the downstroke. A tip vortex and trailing edge vortex can also be observed. As one can expect, the downwash is located directly below the hawkmoth's body during hawkmoth hovering flight. At 2 m/s forward flight, the downwash is situated both below and behind the hawkmoth. When the flight speed increase to 4 m/s, a chain of vortex tubes is observed behind the insect body. This change in wake structures can be explained by a combination of flight speed and the induced flow generated by flapping wings at each flight speed. As the hawkmoth's flight speed increases, the wing kinematics shift from a 'back-and-forth' motion to an 'up-and-down' motion. During 4 m/s forward flight, the hawkmoth's wing pitching angle is roughly parallel to the incoming flow. Combined with such a high forward flying speed, vortices are shed directly behind the hawkmoth.

Figure 19 shows the vortex structures present at mid-downstroke ($t/T=0.25$) for hovering, 2 m/s forward flight, and 4 m/s forward flight. The downstroke for all three flight speeds is accompanied by the formation of a large LEV and TV. A TEV is also present during the downstroke for all three flapping cases. However, for 4 m/s forward flight, the size of the TEV is significantly smaller than for hovering and 2 m/s forward flight. Zheng et al.[15] and Aono et al.[14] have noted that during hovering flight, the LEV, TV, and TEV form a horseshoe-shaped pattern around the hawkmoth wing during the downstroke. For the current study, this pattern can be clearly observed during hovering and 2 m/s flight, but the much smaller TEV for 4 m/s flight prevents the formation of a full horseshoe pattern. This can be partially explained by the stretching and distortion of the vertex structures due to the strong convection at 4 m/s.

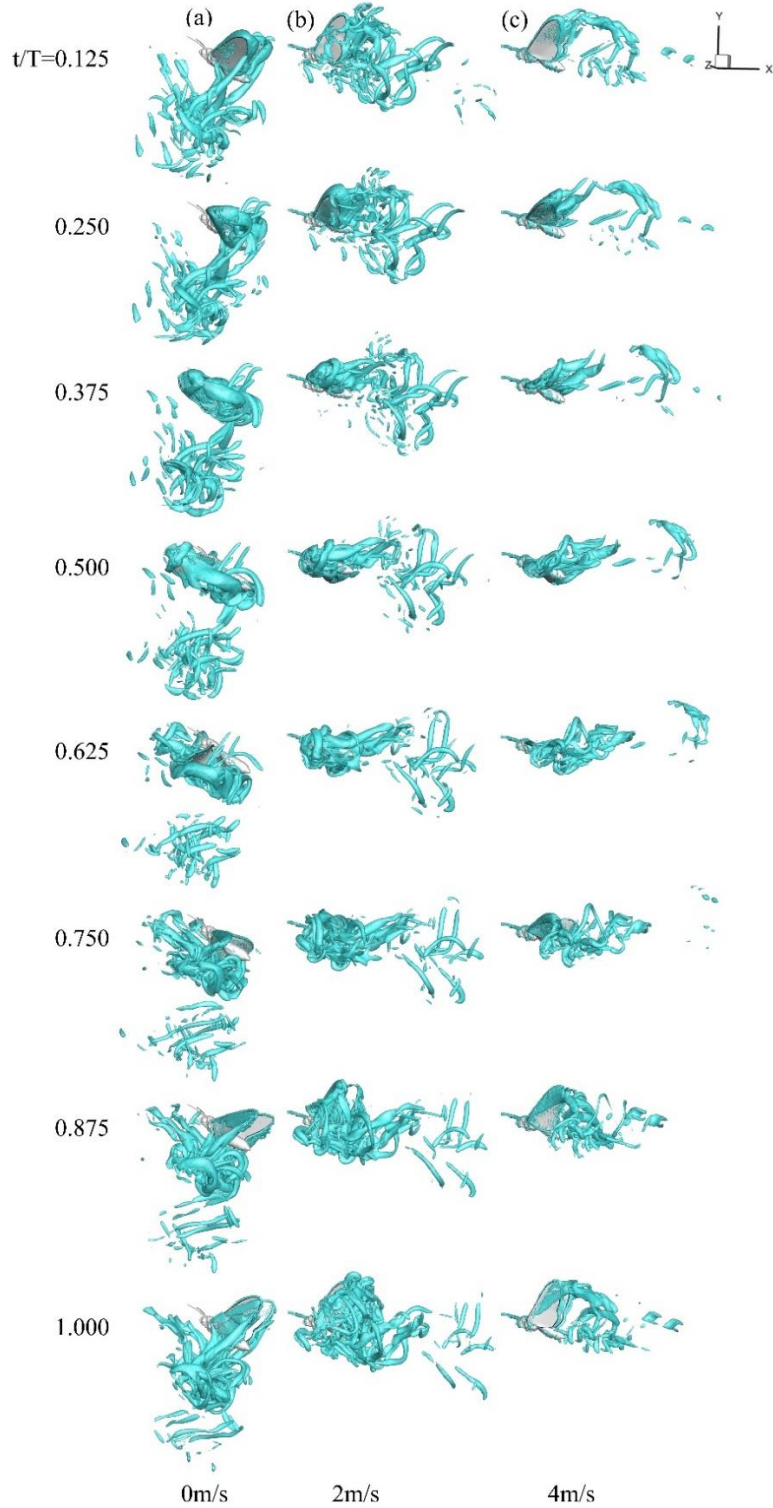


Figure 18. Q-criterion vortex structures for (a) hawkmoth hovering, (b) 2 m/s forward flight, and (c) 4 m/s forward flight. The iso-surface of $Q = 10(\bar{U}_{tip} / R)^2$ was used to plot the vortex structures. See movie 1 in the supplemental material for simulated flow animations [21].

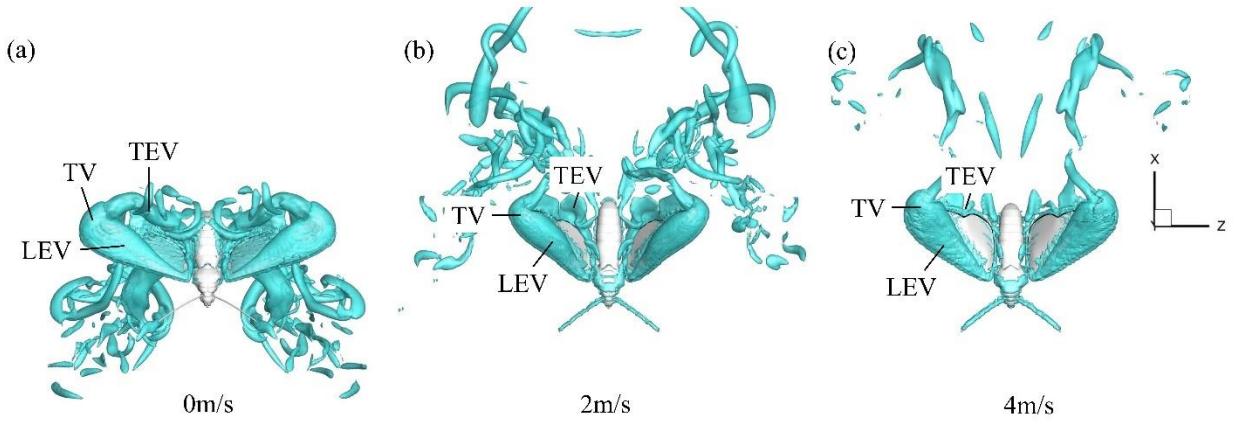


Figure 19. Top view of vortex structure generated at the mid-downstroke ($t/T=0.25$) for (a) hawkmoth hovering, (b) 2 m/s forward flight, and (c) 4 m/s forward flight. The iso-surface of $Q = 10(\bar{U}_{tip} / R)^2$ was used to plot the vortex structures.

Next, we visualize the distribution of lift force generation on the wing surface. Figure 20 shows mean lift production on the wing surface during the downstroke and upstroke, respectively, for all simulated flight motions. Lift production during the hovering downstroke increases along the wingspan, with the highest amount of lift produced near the wing tip and the lowest lift produced near the wing root. However, during the downstroke for the forward flying cases, the greatest lift is produced along the leading edge of the wing, and the lowest lift is produced along the trailing edge. We believe that this difference is linked to the location of the maximum flow velocity for each flight case. During hovering flight, the maximum flow velocity is generated by the wing tip, resulting in the greatest lift generation near this region. However, during forward flight, the flapping wing encounters the incoming flow which will enhance the development of the LEV along the wingspan. In addition, as the flying speed gradually increases, hawkmoths tilt the stroke plane more vertically, which further promotes lift generation during the downstroke. As a result, there is a larger LEV along the spanwise portion of the wing, and a greater portion of the overall lift is generated during the forward flight downstroke.

The most significant difference in the lift generation between hovering and forward flight appears during the upstroke. The hovering upstroke is similar to the hovering downstroke, with lift production increasing along the wingspan, resulting in greatest lift close to the wing tip. However, the lift production during the forward flight upstroke displays an opposite pattern. For 2 m/s and 4 m/s forward flight, significant negative lift is produced near the wing tip, while slight amount of positive lift production is seen close to the wing root. This reversal of lift production during the upstroke is evidence for a different mechanism of lift production for hovering compared to forward flight. For both 2 m/s and 4 m/s forward

flight, approximately 75% of the wing surface produces negative lift during the upstroke. This observation is reflected in Figure 12 (b-c), which shows positive lift generation during the downstroke and negative lift generation during the upstroke for both 2 m/s and 4 m/s forward flights. However, during the hovering upstroke, the entire wing surface shows positive lift production. This corresponds to Figure 12 (a), which shows that positive lift is generated during both the upstroke and downstroke for hovering flight.

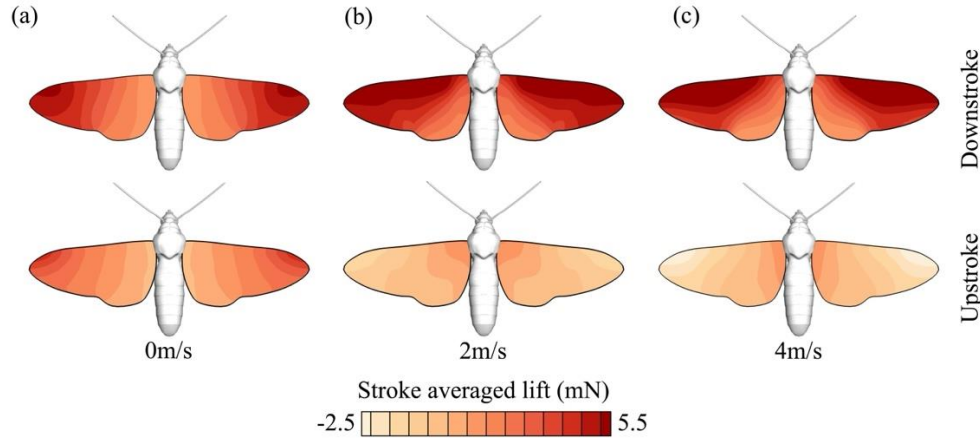


Figure 20. Stroke-averaged lift force distribution on the wing surfaces during downstroke and upstroke for (a) hovering, (b) 2 m/s forward flight, and (c) 4 m/s forward flight.

3.3 Comparison of hawkmoths and other flying animals

We have observed that as the hawkmoth's advance ratio J increases along with flight speed, lift production is increasingly dominated by the downstroke. At hovering ($J=0$), both the downstroke and upstroke provide positive contributions to the total lift generation for the flapping cycle. However, at 2 m/s ($J=0.41$) and 4 m/s ($J=0.85$) forward flight, the downstroke produces 100% of the overall lift, and negative lift is generated during the upstroke.

Several previous studies [2, 3, 49, 55] have also commented on the relationship between an insect's advance ratio and the downstroke's contribution to total lift production. The results of the current study are qualitatively consistent with results obtained by Sun & Wu [55] for a model fruit fly. They found that for an advance ratio of 0.13, the downstroke contributes 75% of the total lift production. For an advance ratio of 0.53, the downstroke contributes 100% of the total lift, and negative lift is generated during the upstroke. Dudley & Ellington [3] also found that for a relatively high advance ratio of 0.59, 100% of a bumblebee's total lift is produced during the downstroke, but they did not indicate whether the upstroke generates negative lift in their study.

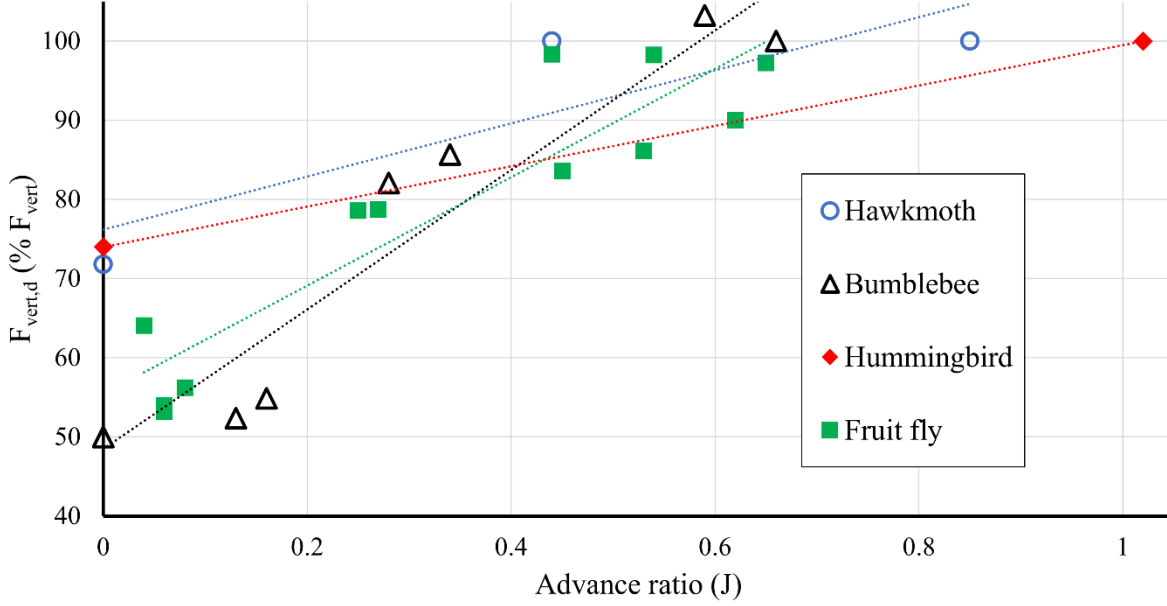


Figure 21. Relationship between the advance ratio (J) and $F_{\text{vert},d} (\% F_{\text{vert}})$ for different small animal species, including hawkmoth (current study), bumblebee[2, 3], hummingbird[5, 6], and fruit fly[4]. Least-squares trendlines are shown as dashed lines for each species.

Following the definition presented in the literature [3], we evaluated the percentage of the vertical force generated during the downstroke ($F_{\text{vert},d}$) over the vertical force generated during the entire cycle (F_{vert}) as a function of the advance ratio (J) across different species. Figure 21 shows the relationship between J and $F_{\text{vert},d} (\% F_{\text{vert}})$ for a variety of small flying animals. This plot shows that as an animal's advance ratio increases, the downstroke plays an increasingly important role in the overall lift production. The plot also shows that if the advance ratio is sufficiently high, the downstroke generates 100% of the total lift. In addition, a least-squares trendline is included for each species. Comparing the results for each species shows that as a flying animal's weight increases, the slope of this trendline generally decreases.

Based on the results from the current study, we suspect that maximum flying speed limitation is due to changes in a flying animal's wing kinematics as its advance ratio increases. As the flight speed gradually increases, the animal must find a way to minimize drag during its entire flapping cycle to prevent itself from blowing away in the incoming flow. To minimize the magnitude of the instantaneous drag force generated during the downstroke, the animal has to reduce its wing pitching angle by orienting its wings roughly parallel to the flow direction, while still maintaining sufficient angle of attack for lift generation. As the advance ratio continuously increases with flight speed, a significant amount of negative lift force starts to appear during the upstroke resulting from a negative angle of attack. As a consequence, the positive lift generated during the animal's downstroke is not sufficient to overcome the body weight together with the negative lift generated during the upstroke. However, increasing downstroke lift would also increase

downstroke drag, requiring more upstroke thrust and resulting in more upstroke negative lift. Thus, these kinematic limitations result in a limit to its maximum forward flying speed as we and others observe in wind tunnel flight studies [11, 12]. Compared to birds and bats, insects are more strongly limited by these effects because they cannot reconfigure their wings during the stroke cycle. For example, birds typically flex their wings at the wrist joint during the upstroke, reducing wing span and area [56]. Despite having inflexible wings in comparison to most other bird species, even hummingbirds exhibit such an ability and increasingly reduce wing span during the upstroke as flight speed increases [57]. Insects have no such ability, and thus might generally exhibit lower maximum flight speeds than flying vertebrates of similar wing loading.

4 Conclusions

We have numerically investigated the unsteady aerodynamics of hawkmoth flight across a range of flying speeds (0 m/s – 4 m/s). Flapping wing kinematics of hawkmoths have been reconstructed using high-speed wind tunnel recordings. An in-house immersed-boundary-method-based CFD solver has been used to simulate hawkmoth’s flight. Results show that as the hawkmoth transitions from hovering to forward flight, the hawkmoth’s stroke plane angle increases and its upstroke wing pitch angle decreases. These kinematic changes lead to differences in aerodynamic force production and power consumption between hovering and forward flight.

During hawkmoth hovering, significant lift is generated during both the downstroke and upstroke, with the downstroke contributing around 72% of the total lift. At 2 m/s and 4 m/s forward flight, however, the downstroke provides all of the lift, and negative lift is generated during the upstroke. Detailed analysis has been performed on the vortex formation and force distributions on the wing surfaces. Our results indicated that the power consumption seem not to restrict forward flight speed in hawkmoths. Instead, the hawkmoth has to manage drag during its downstroke to prevent large, unstable body oscillations at higher forward flying speeds. To reduce drag force generated during each downstroke, the forward flying hawkmoth must maintain a small wing pitching angle that is roughly parallel to the flying direction. Due to biological limitations, the hawkmoth cannot drastically alter its wing pitching angle during the short period of the wing reversal. As a result, a forward flying hawkmoth’s wings have to remain approximately horizontal respect to the stroke plane during the upstroke, which leads to a negative lift force generation. As the flying speed increases, the lift generated during the downstroke cannot balance with the body weight together with the negative lift generated during the upstroke. This effect limits high speed flight in hawkmoths, and highlights the importance of reconfigurable wings to the wide range of flight speeds achieved by flying vertebrates.

Acknowledgments

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