Lift vs. drag based mechanisms for vertical force production in the smallest flying insects

S. K. Jones^{1*}, R. Laurenza¹, T. L. Hedrick², B. E. Griffith¹, L. A. Miller^{1,2}

Author addresses: ¹ *Department of Mathematics, University of North Carolina, Chapel Hill, NC 27599,*

USA, ²*Department of Biology, University of North Carolina, Chapel Hill, NC 27599, USA*

**Corresponding author (skjohnsn@email.unc.edu, +1-919-452-5238)*

Abstract

We used computational fluid dynamics to determine whether lift- or drag-based mechanisms generate the most vertical force in the flight of the smallest insects. These insects fly at Re on the order of 4–60 where viscous effects are significant. Detailed quantitative data on the wing kinematics of the smallest insects is not available, and as a result both drag- and lift-based strategies have been suggested as the mechanisms by which these insects stay aloft. We used the immersed boundary method to solve the fully-coupled fluid-structure interaction problem of a flexible wing immersed in a two-dimensional viscous fluid to compare three idealized hovering kinematics: a drag-based stroke in the vertical plane, a lift-based stroke in the horizontal plane, and a hybrid stroke on a tilted plane. Our results suggest that at higher Re , a lift-based strategy produces more vertical force than a drag-based strategy. At the Re pertinent to small insect hovering, however, there is little difference in performance between the two strategies. A drag-based mechanism of flight could produce more vertical force than a lift-based mechanism for insects at $Re < 5$; however, we are unaware of active fliers at this scale.

Key index words or phrases: insect flight, computational fluid dynamics, immersed boundary method, biomechanics

1. Introduction

Though their flight mechanisms are not well studied, the smallest flying insects are of significant agricultural and ecological importance. For example, thrips are a common agricultural pest (Palmer, Reddy et al. 1990; Crespi, Carmean et al. 1997), and parasitoid wasps have the potential to be used for natural biological control of agricultural pests (Austin and Dowton 2000). Understanding the aerodynamics of flapping flight at this small scale may offer further insight into the aerodynamical limits of flight of these organisms and lead to improved dispersal strategies for biological control. Previous work has shown that the flight kinematics and aerodynamics of the smallest insects may be significantly different than that of their larger counterparts (Weis-Fogh 1973; Wang 2000; Sunada, Takashima et al. 2002; Miller and Peskin 2004; Miller and Peskin 2005; Miller and Peskin 2009). Because of their small size and high wing beat frequency, detailed quantitative data on the wing kinematics of the smallest insects is not readily available (Sane 2003; Miller and Peskin 2009). As a result, there has been much debate and speculation about the flight strategies employed by these insects. Traditional lift-

based strokes in the horizontal plane and less-traditional swimming-like strokes in the vertical plane have both been suggested. In this study, we used computational fluid dynamics to investigate whether lift- or drag-based mechanisms generate the most vertical force for scales relevant to tiny insects.

The smallest flying insects are on the order of 1 mm in length, and have been reported to flap their wings at frequencies greater than 200Hz (Santhanakrishnan, Robinson et al. 2014) and possibly as high as 400Hz (Weis-Fogh 1973). At this scale and wingbeat frequency, viscous forces are significant, and the relevant Reynolds numbers (Re) are on the order of 4-60. A chord-based Re is commonly used to quantify the ratio of inertial to viscous forces for flying insects (Fig 1a):

$$Re = \frac{\rho U c}{\mu}, \quad (1)$$

where ρ is the fluid density, U is the characteristic velocity of the wing, c is the chord length, and μ is the dynamic viscosity. Well-studied insects, such as *Drosophila* (Dickinson and Gotz 1993; Dickinson, Lehmann et al. 1999) and *Manduca sexta* (Usherwood and Ellington 2002; Hedrick, Cheng et al. 2009), fly at a Re on the order of 100 and 1000, respectively. Smaller and less well-studied insects, such as thrips and fairy flies, operate at a $Re < 10$. At this low Re range, the lift to drag ratio decreases significantly (Wang 2000; Miller and Peskin 2004) and the flight aerodynamics and wing kinematics differ from those of larger insects.

Video recordings of free-flying tiny insects require high-speed cameras equipped with macro-lenses and high lighting; even with an ideal set-up, the field of view is very narrow. Consequently, very few tiny insect species have been filmed to date. Those that have been filmed include *Encarsia formosa* (Weis-Fogh 1973), *Trialeurodes vaporarioru* (Weis-Fogh 1975), *Thrips physapus* (Ellington 1984), and *Muscidifurax raptor* and *Nasonia vitripennis* (Miller and Peskin 2009). All of these species appear to use the clap and fling mechanism; however, a quantitative description of clap and fling kinematics for these insects is still unavailable. While clap and fling is surely an important mechanism in small insect flight, it may not be the only flight strategy used by these organisms.

At this point, it would be useful to define conventional terminology that will be used throughout this paper (Fig 1b). Lift is the component of force that is normal to the oncoming flow with respect to the motion of the wing, whereas drag is the component of force parallel to oncoming flow. In the case of a hovering insect, lift and drag are perpendicular and parallel, respectively, to the direction of wing motion. Intuitively, one might expect that lift is always “up”; however lift may also be entirely downward or even horizontal since it is defined with respect to the direction of movement of the wing. To help keep this clear, we will also define two other forces: vertical force (F_V) and horizontal force (F_H). F_V is that parallel to the direction of gravity,

71 whereas F_H is normal to gravity. Unlike lift and drag, F_V and F_H always face the same direction
72 with respect to the global frame. We will adhere to these definitions of lift, drag, F_V and F_H as we
73 investigate force production and flight aerodynamics of the smallest insects.

74 A lift-based strategy for small insect flight became widely accepted following Weis-Fogh's
75 influential 1973 paper that described clap and fling (Weis-Fogh 1973). Subsequently, a
76 combination of work supported the idea that insects increase the lift generated during flight by
77 clapping their wings together at the end of upstroke and flinging them apart at the beginning of
78 the downstroke (Lighthill 1973; Maxworthy 1979; Ellington 1984; Ellington 1984; Spedding and
79 Maxworthy 1986; Sun and Xin 2003; Lehmann, Sane et al. 2005; Miller and Peskin 2005; Sun
80 and Yu 2006; Lehmann and Pick 2007; Miller and Peskin 2009). However, very large forces are
81 required to fling the wings apart at the low Re relevant to the smallest insects (Miller and Peskin
82 2005).

83 A drag-based strategy for small insect flight was first suggested when Horridge proposed that
84 small insects might generate vertical force by 'swimming' or paddling through the air, rather
85 than using a lift-based aerofoil action (Horridge 1956). This strategy has been observed in larger
86 insects, such as butterflies, which use a nearly-vertical stroke plane (Ellington 1984). A
87 computational study showed that the importance of drag is frequently underestimated in hovering
88 flight, with an idealized dragonfly wing motion supporting three quarters of the insect's weight
89 with drag (Wang 2004). Recently, a drag-based, swimming-like mode of forward flight was
90 observed in the fruit fly (Ristroph, Bergou et al. 2011). However, most studies of insect flight
91 focus on insects with $Re > 100$. With the challenges associated with generating lift at low Re , it
92 could be beneficial for the smallest insects to use a drag-based motion to generate some or all of
93 its vertical force; however, this has not been rigorously investigated.

94 Computational fluid dynamics provide a convenient method to investigate the aerodynamics of
95 flying insects where direct experimentation would be difficult. Computational studies also have
96 the advantage of being able to explore parameter space and optimize the aerodynamics of the
97 theoretical computational flier (Berman and Wang 2007; Nakata and Liu 2012; Zheng, Hedrick
98 et al. 2013). Most of the computational studies to date have focused on larger insects (Bush and
99 Baeder 2007; Ramamurti and Sandberg 2007; Nakata and Liu 2012; Zheng, Hedrick et al. 2013;
100 Xu and Sun 2014), but some have investigated fliers at $Re < 100$ (Wang 2000; Miller and Peskin
101 2004; Wang, Birch et al. 2004; Miller and Peskin 2005; Miller and Peskin 2009).

102 The goal of this study was to determine whether lift- or drag-based mechanisms generate the
103 most vertical force at $Re < 100$. We used the immersed boundary method to solve the fully
104 coupled fluid-structure interaction problem of a flexible wing immersed in a 2D viscous fluid.
105 We used this method to (1) compare three idealized 2D hovering kinematics: a drag-based stroke
106 in the vertical plane, a lift-based stroke in the horizontal plane, and a hybrid stroke on a tilted
107 plane; (2) compare faster and slower downstroke velocities; and (3) compare flexible and rigid
108 wings. F_V and F_H were calculated as functions of time, and we determined how the structure of

the vortex wake influenced the forces. Net vertical force and the ratio of vertical force to total force generated by these strokes were compared over a range of Re from 1 to 200.

2. Methods

2.1 Prescribed wing kinematics. To investigate the role of lift and drag in vertical force production, we considered three idealized stroke kinematics: a horizontal lift-based stroke, a vertical drag-based stroke, and a tilted hybrid stroke. The horizontal stroke approximates fruit fly kinematics (Fig 2a), and lift is used to generate vertical force. The vertical stroke is a theoretical stroke (Fig 2b), idealized to give the most possible drag-based vertical force and is similar to rowing with feathering on the upstroke. The hybrid stroke approximates dragonfly kinematics (Fig. 2c), and uses a combination of lift and drag to generate vertical force.

We explored the forces produced by these strokes with a numerical simulation of a moving elastic wing immersed in a viscous fluid. The simplified insect wing kinematics used in this paper are similar to those used in previous computational studies (Wang 2000; Wang 2004; Wang, Birch et al. 2004) to investigate hovering flight aerodynamics. A two-dimensional cross-section of the wing chord was used for all investigations, and we use the term “wing” in the remainder of the paper to describe a wing’s cross section. The kinematics of the wing were defined as follows:

$$[x(t), y(t)] = \frac{A_0}{2} (1 + \cos(2\pi ft)) [\cos(\beta), \sin(\beta)], \quad (2)$$

$$\alpha(t) = \alpha_0 + B \sin(2\pi ft), \quad (3)$$

in which $[x(t), y(t)]$ is the position of the centre of the chord at time t , A_0 is the amplitude of translation, f is the frequency, β is the stroke plane angle, α is the chord orientation relative to β (i.e. the angle of attack), α_0 is the mean angle of attack, and B is the amplitude of rotation. In all computations, $f=1$, $B=\pi/4$ and $A_0/c=2.5$, where c is the chord length. By changing α_0 and β , we prescribe the motion of three idealized strokes: the horizontal stroke ($\alpha_0=90^\circ$, $\beta=0^\circ$), the vertical stroke ($\alpha_0=45^\circ$, $\beta=90^\circ$), and the tilted stroke ($\alpha_0=60^\circ$, $\beta=62.8^\circ$).

2.2 Numerical method. We used the immersed boundary method (Peskin 2002) to model two-dimensional insect wings immersed in a viscous, incompressible fluid. The immersed boundary method has been used to model a variety of biological fluid dynamics problems, including aquatic locomotion (Fauci and Peskin 1988; Fauci and Fogelson 1993), insect flight (Miller and Peskin 2004; Miller and Peskin 2005; Miller and Peskin 2009), bacterial flagella (Lim and

Peskin 2012; Maniyeri, Suh et al. 2012), jellyfish swimming (Herschlag and Miller 2011) and ciliary driven flows (Grunbaum, Eyre et al. 1998).

The equations of fluid motion are as follows:

$$\rho \left(\frac{\partial \mathbf{u}(\mathbf{x}, t)}{\partial t} + \mathbf{u}(\mathbf{x}, t) \cdot \nabla \mathbf{u}(\mathbf{x}, t) \right) = -\nabla p(\mathbf{x}, t) + \mu \Delta \mathbf{u}(\mathbf{x}, t) + \mathbf{f}(\mathbf{x}, t), \quad (4)$$

$$\nabla \cdot \mathbf{u}(\mathbf{x}, t) = 0, \quad (5)$$

where $\mathbf{u}(\mathbf{x}, t)$ is the fluid velocity at position $\mathbf{x}=[x, y]$ and time t , $p(\mathbf{x}, t)$ is the pressure, $\mathbf{f}(\mathbf{x}, t)$ is the force per unit area applied to the fluid by the immersed boundary.

The interaction equations between the fluid and the boundary are given by:

$$\mathbf{f}(\mathbf{x}, t) = \int \mathbf{F}(r, t) \delta[\mathbf{x} - \mathbf{X}(r, t)] dr, \quad (6)$$

$$\frac{\partial \mathbf{X}(r, t)}{\partial t} = \mathbf{u}(\mathbf{X}(r, t), t) = \int \mathbf{u}(\mathbf{x}, t) \delta(\mathbf{x} - \mathbf{X}(r, t)) d\mathbf{x}, \quad (7)$$

in which $\mathbf{F}(r, t)$ is the force per unit length applied to the body as a function of Lagrangian position r and time t , $\delta(\mathbf{x})$ is a two-dimensional Dirac delta function, and $\mathbf{X}(r, t)$ gives the physical coordinates at time t of the material point labelled by the Lagrangian parameter r . Equation 6 spreads force from the boundary to the fluid grid, and Equation 7 evaluates the local fluid velocity at the boundary. The boundary is then moved at the local fluid velocity, and this enforces the no-slip condition. These equations act to couple the Lagrangian and Eulerian variables. Details on the discretization used in these simulations have been described previously (Peskin and McQueen 1996; Griffith, Hornung et al. 2007; Miller and Peskin 2009).

The dimensionless equation describing a two-dimensional elastic wing immersed in a fluid can be written as follows:

$$\mathbf{F}' = k'_{beam} \frac{\partial^2}{\partial r^2} (\hat{k} \hat{n}) - \frac{\partial}{\partial r} (T \hat{r}) \quad (8)$$

Where $\mathbf{F}'$ is the dimensionless force applied to the wing, k'_{beam} is the dimensionless bending stiffness, $\hat{k}$ is the curvature, $\hat{n}$ is the unit vector pointing normal to the wing, T is the tension, and $\hat{r}$ is the unit vector tangent to the wing. The dimensionless bending stiffness can be written as:

$$k'_{beam} = \frac{k_{beam}}{\rho U_{rms}^2 c^3} \quad (9)$$

Where k_{beam} is the dimensional flexural stiffness and U_{rms} is the root mean square of the velocity of the center of the chord. In order to compare the forces from the computations, instantaneous forces experienced by the wing were non-dimensionalized by $0.5\rho U_{rms}^2 c$. C_V and C_H denote the vertical and horizontal force coefficients, respectively.

In this study, we used a distributed-memory parallel implementation of the immersed boundary method with Cartesian grid adaptive mesh refinement, called IBAMR (Griffith, Hornung et al. 2007). IBAMR has been used to investigate a variety of biological fluid dynamics problems, including modelling spined cells (Nguyen, Karp-Boss et al. 2011), biofilm deformation in capillaries (Vo and Heys 2011), lamprey swimming (Tytell, Hsu et al. 2010), and heart valves (Griffith, Luo et al. 2009; Griffith 2012). Our computational 2D wing was immersed in a fluid domain that was 20 chord lengths wide and high. The adaptive method used four grid levels to discretize the Eulerian equations with a refinement ratio of 4 between levels. Regions of fluid that contained the wing or vorticity above a threshold were discretized at the highest refinement. The effective resolution of the finest level of the grid corresponded to that of a uniform 512×512 discretization for $Re \leq 100$ and a uniform 1024×1024 discretization for $Re > 100$. The boundary conditions were set to no-slip ($\mathbf{u}=0$) on all sides of the computational domain. Other simulation-specific numerical parameters are listed in Table 2.

To investigate the role of lift and drag in tiny insect flight, we considered three idealized wing strokes for Re ranging from 1 to 200. We defined Re as

$$Re = \frac{\rho U_{max} c}{\mu} = \frac{\rho \pi f A_0 c^2}{\mu}, \quad (10)$$

in which U_{max} is the maximum velocity of the wing during a stroke. The Re was varied by changing μ while holding all other parameters constant.

The lift-to-drag ratio is one common metric of comparison used in studies of hovering. The lift-to-drag ratio is not an appropriate metric in this study, however, because we investigated wing kinematics that predominantly use drag to generate vertical force. Because we are studying very different types of strokes, comparing them in an equal way is challenging: C_V and C_H are zero at different points in the strokes, and net drag and net lift are zero for the horizontal and vertical strokes, respectively. However, our main motivation is to determine the amount of vertical force that can be generated compared to the total amount of force. For that reason, we chose to compare the three strokes using the ratio of net vertical force to net total force ($\overline{C_V}/\overline{C_T}$) over the third and fourth wing stroke. C_T determines the magnitude of the force that the muscles have to produce during flight. $\overline{C_V}/\overline{C_T}$ gives us a metric for how much of that force goes toward C_V .

2.3 Grid convergence study. To test for spatial convergence, we compared four effective fine-grid resolutions: a uniform 256×256 discretization, a uniform 512×512 discretization, a uniform 1024×1024 discretization and a uniform 2048×2048 discretization. All four resolutions used the horizontal stroke kinematics described in Fig. 2a and were evaluated at $Re=10$, $Re=100$, and $Re=200$. We chose to complete the convergence study over a range of Re because more refined grids are often necessary at high Re , where the boundary layers around wings are smaller, and the error at the boundary is more significant. The highest Re demonstrated the most error, because of the challenge of accurately resolving the boundary layers and the separation of vortices. C_V and C_H as functions of dimensionless time show small deviations between the grid resolutions during periods of wing acceleration and deceleration (Fig. 3a-c); however, the coefficients show overall good agreement. We compared the four grid resolutions by calculating the average percent difference in force between the selected grid and the next finest grid over the first two wingbeats (Table 3). For comparison, the average percent difference between different Re over two wing strokes for the horizontal stroke is shown in Table 4. Effective 512×512 grid discretization was used for all other simulations with $Re \leq 100$, and 1024×1024 grid discretization was used for all other simulations with $Re > 100$ in this paper. These grids were chosen because the average percent difference in force between the selected grid and the next finest grid is $\leq 5\%$.

2.4 Comparison to existing numerical data. To check our method, we compared our model of the horizontal stroke to the numerical model given by Wang at $Re=150$ (Wang 2004). C_V and C_H as functions of time are shown (Fig. 4). Overall, there was good agreement between our IBAMR simulation and the numerical simulation described by Wang. The differences can probably be attributed to differences in the numerical models—our wing is a flexible two-dimensional plate, while Wang’s is a rigid ellipse.

3. Results

3.1 Comparison of three idealized hovering kinematics. Simulations using the kinematics described in the methods section were performed for Re ranging from 1 to 200. Each simulation included four stroke cycles. Only the third and fourth stroke cycles that exhibited periodic behaviour were used to obtain net aerodynamic forces.

C_V and C_H as functions of dimensionless time are shown for $Re = 1, 5, 10$, and 100 for the horizontal stroke (Fig. 5), the tilted stroke (Fig. 6) and the vertical stroke (Fig. 7). The shapes of the graphs of the horizontal and tilted strokes at $Re=100$ were similar to those obtained by Wang at $Re=150$ (Wang 2004), and the magnitude and trends for the horizontal stroke were consistent with those found by Miller and Peskin for a similar horizontal stroke (Miller and Peskin 2004). For all stroke types in this Re range, the magnitude of the instantaneous force coefficients decreased with increasing Re .

For the horizontal stroke (Fig. 5), C_V was positive for nearly the entire stroke, whereas for the tilted and vertical strokes (Figs. 6-7), C_V was positive during the downstroke and negative during the upstroke. In the tilted and vertical strokes, C_V peaked during mid-translation when the wing was moving most quickly. This was also the case for the horizontal stroke at low Re . At $Re=100$, C_V peaked during wing rotation and decreased during the translation phase for the horizontal stroke.

For the horizontal stroke, peak C_H was much larger in magnitude than peak C_V , whereas for the tilted and vertical strokes peak C_V was larger in magnitude than peak C_H . For the horizontal and tilted strokes at lower Re , C_H peaked during translation. At $Re=100$, C_H increased during wing rotation and decreased during the translation phase of the stroke. For the vertical stroke, the peaks in C_H correspond to forces generated during wing rotation for all Re investigated. During translation, we expect C_H to be negligible due to the orientation of the wing during the vertical strokes.

The basis for some of these differences can be seen by comparing vorticity plots of the fluid flow around the wing at $Re=10$ and $Re=100$ (Figs 8-10). For all strokes at $Re=10$ (Fig 8A, 9A, 10A), leading (LEV) and trailing (TEV) edge vortices formed during wing rotation at the beginning of downstroke (i). These vortices remained attached during downstroke (ii), and were shed at the end of downstroke during wing rotation (iii). New LEVs were formed during wing rotation and remained attached until the wing rotated at the beginning of the next downstroke (iv).

In contrast, vortex shedding played a significant role in force generation at $Re=100$. In the horizontal stroke (Fig 8B), at the beginning of downstroke, a LEV and a TEV formed (i). Midway through downstroke, the LEV remained attached while the TEV was shed (ii). During wing rotation and the beginning of upstroke, the vortices were shed and a new LEV and TEV were formed as the wing travelled back through its wake (iii). Midway through upstroke, the LEV remained attached while the TEV was shed generating positive C_V (iv). The tilted stroke behaved similarly to the horizontal stroke at $Re=100$ (Fig 9B). At the end of downstroke, the shed vortices travelled downward more quickly for the tilted stroke than for the horizontal stroke, which matched results found by Wang (Wang 2004). In the vertical stroke at $Re=100$ (Fig 10B), a larger LEV formed during wing rotation at the beginning of downstroke (i), and remained larger during downstroke (ii). During wing rotation and the beginning of upstroke, the vortices were shed (iii). The shed vortices travelled downward more quickly for the vertical stroke than for the other strokes. During upstroke (iv), the wing was oriented parallel to the direction of movement, and vorticity was shed asymmetrically, generating some C_H .

The three strokes were evaluated at Re ranging from 1 to 200. C_V was averaged over the 3rd and 4th wingbeats and plotted as functions of Re for each of the types of stroke (Fig 11). Similarly, the $\overline{C_V}/\overline{C_T}$ (Eq. 9) as functions of Re are shown in Fig 12. The horizontal stroke generated more $\overline{C_V}$ than the other strokes at $Re > 2$, whereas the vertical stroke generated the most $\overline{C_V}$ at $Re < 2$. The vertical stroke generated the least $\overline{C_V}$ at $Re > 10$. The vertical stroke had the greatest

$\overline{C_V}/\overline{C_T}$ at $Re < 5$; however, it had the lowest $\overline{C_V}/\overline{C_T}$ at $Re > 20$. The horizontal stroke had the greatest $\overline{C_V}/\overline{C_T}$ at $Re > 5$. $\overline{C_V}/\overline{C_T}$ increased with Re , and at $Re > 20$ $\overline{C_V}$ increased with Re for all stroke types. Both $\overline{C_V}$ and $\overline{C_V}/\overline{C_T}$ began to plateau at $Re > 100$ as viscous effects become less significant. It is worthwhile to note that these results include unsteady effects, and much of the C_V for the lower Re was generated during wing rotation at the end of each stroke. There was a large increase in $\overline{C_V}$ as Re decreased below 10. This matches results of Miller and Peskin: dimensionless drag remained relatively constant with decreasing Re , then increased rapidly for $Re < 10$ (Miller and Peskin 2004). This likely happens because at these low Re most C_V is generated as a result of shearing the viscous fluid during wing rotation.

3.2 Faster downstroke. Bennet further suggested that a faster downstroke velocity would enhance C_V produced by a drag-based mechanism (Bennet 1973). Despite observed insects having faster upstrokes, rather than downstrokes (Table 1), we wanted to investigate what effect a faster downstroke would have on C_V produced by tiny insects using a drag-based mechanism.

We evaluated the vertical stroke at different ratios (η) of the downstroke velocity to the upstroke velocity. Here,

$$\eta = \frac{T_{upstroke}}{T_{downstroke}},$$

where $T_{downstroke}$ and $T_{upstroke}$ are the times to complete downstroke and upstroke, respectively. Re was calculated as before. C_V was evaluated for η ranging from 0.75 to 2, at Re from 1 to 100. C_V and C_H as functions of dimensionless time are shown for all η at $Re=10$ and $Re=100$ (Fig 13a&b). The magnitude of C_V during downstroke increased with increasing η , however the duration of the downstroke decreased. Similarly, the magnitude of C_V during upstroke decreased with increasing η ; however, the duration of the upstroke increased. In all Re investigated, $\overline{C_V}$ increased with η , and the $\eta=2$ case had a greater $\overline{C_V}$ than the corresponding symmetric horizontal stroke (Fig 14). Similarly, $\overline{C_V}/\overline{C_T}$ increased with η ; however, at higher Re the horizontal stroke had a greater $\overline{C_V}/\overline{C_T}$ than all vertical strokes regardless of η (Fig 15). At $Re \leq 10$, the $\eta=2$ case had a greater $\overline{C_V}/\overline{C_T}$ than the horizontal stroke. The increase in $\overline{C_V}$ and $\overline{C_V}/\overline{C_T}$ was Re dependent—the magnitude of the effect decreased with decreasing Re . At the Re of the smallest insects, the increase in performance was small. Interestingly, *Encarsia formosa* has a faster upstroke than downstroke with $\eta=0.75$ (Weis-Fogh 1973). A vertical stroke with $\eta=0.75$ had a lower $\overline{C_V}$ and $\overline{C_V}/\overline{C_T}$ than $\eta=1$.

The aerodynamic basis for these changes in $\overline{C_V}$ and $\overline{C_V}/\overline{C_T}$ can be seen by comparing the vorticity field when $\eta=1$ (Fig 10) and $\eta=2$ (Fig 16). When $\eta=2$ at $Re=10$, larger vortices were formed during downstroke (Fig16Aii), and consequently larger vortices were shed during wing rotation at the end of downstroke (Fig16Aiii). The effect of η was even more pronounced at larger Re . When $\eta=2$ at $Re=100$, larger vortices were also formed during downstroke (Fig16Bii)

and shed during wing rotation (Fig16Biii). The shed vortices travelled downward twice as fast when $\eta=2$ (Fig 16Biv).

3.3 Flexible wings. We also expect that flexibility will play a role in wing performance. Flexibility of biological structures has been demonstrated to reduce drag in a number of studies (Koehl 1984; Vogel 1989; Etnier and Vogel 2000; Alben, Shelley et al. 2002; Alben, Shelley et al. 2004; Miller, Santhanakrishnan et al. 2012). To compare a flexible wing to the rigid case, we selected $k'_{beam}=31$. We chose this value to represent a case in which deformations are very small but some bending does occur (Fig 17). The vertical stroke experienced bending of $\sim 10^\circ$ during mid-downstroke at $Re=10$. In the flexible wing, the leading edge of the wing (1/5 of the chord length) remained rigid, whereas the trailing edge of the wing was flexible and allowed to bend as it interacted with the fluid. This represents a simplified way of modelling a stiffer leading edge and flexible trailing edge.

Vorticity fields of the three strokes with flexible wings at $Re=10$ and $Re=100$ (Fig 18-20) can be compared to the rigid cases (Fig 8-10). The flexible wing generated weaker vortices than the rigid wing in all wing strokes. The vortices were also shed more quickly during with rotation in the flexible wing cases.

C_V and C_H as functions of dimensionless time are shown for the flexible and rigid case for all stroke types at $Re=10$ and $Re=100$ (Fig 21). In most cases, the rigid and flexible wings behaved similarly. For the horizontal stroke (Fig 21a), there was a larger peak in C_V following wing rotation at the beginning of downstroke and upstroke in the flexible wing. During wing rotation, the wing bends slightly, and the small increase in C_V was likely a result of the wing returning to a nearly straight configuration during translation. The flexible and rigid tilted strokes (Fig 21b) had similar C_V during downstroke, but the magnitude of the negative C_V during wing rotation and upstroke was smaller for the flexible wing. This is likely due to the flexible wing encountering a smaller wake during the upstroke than the rigid wing. The magnitude of C_H was smaller during both upstroke and downstroke for the flexible wing as a result of drag reduction in the flexible wing. C_V was similar for the flexible and rigid vertical strokes (Fig 21c); however, the plots of C_H are quite different—likely a result of variations in how vortices are shed for the two cases and oscillations in the flexible wing following wing rotation.

There was little difference in $\overline{C_V}$ for the horizontal stroke (Fig 22a), but $\overline{C_V}$ was greater for the flexible wing at all Re for both the tilted and vertical strokes (Fig 22b&c). The greatest increase in $\overline{C_V}$ was seen for the tilted stroke. There was very little difference in $\overline{C_V}/\overline{C_T}$ for flexible and rigid wings using either the horizontal or vertical strokes. The tilted stroke with the flexible wing had a $\sim 20\%$ greater $\overline{C_V}/\overline{C_T}$ than the rigid wing (Fig 23). The increase in $\overline{C_V}/\overline{C_T}$ for the flexible tilted stroke resulted from decrease in negative C_V during upstroke and the decrease in the magnitude of C_H . The magnitude of this improved $\overline{C_V}/\overline{C_T}$ increased with Re .

4. Discussion

The results of this study suggest that: (1) lift-based mechanisms produce more C_V than drag-based mechanisms at $Re > 2$, whereas drag-based mechanisms produce more C_V than lift-based mechanisms at $Re < 2$; (2) lift-based mechanisms have greater $\overline{C_V}/\overline{C_T}$ than drag-based mechanisms at $Re > 5$, while drag-based mechanisms have greater $\overline{C_V}/\overline{C_T}$ than lift-based mechanisms at $Re < 5$; (3) a faster downstroke increases C_V and $\overline{C_V}/\overline{C_T}$ of a drag-based mechanism, although this effect is modest at lower Re ; and (4) flexibility has little effect on a lift-based mechanism, although flexibility increases C_V in a drag-based mechanism and increases both C_V and $\overline{C_V}/\overline{C_T}$ in a stroke that uses both drag- and lift-based mechanisms. At greater Re , a lift-based strategy produces more C_V and has a greater $\overline{C_V}/\overline{C_T}$ than a drag-based strategy; however, at the Re pertinent to small insect hovering there is little difference in performance between the two strategies. According to the results of our study, a drag-based mechanism of flight would have a greater $\overline{C_V}/\overline{C_T}$ than a lift-based mechanism for insects at $Re < 5$, although we are unaware of flapping insect flight at $Re < 5$.

Wang suggested that to benefit from the large drag found in symmetric horizontal strokes, an insect could tilt the downstroke by $\sim 56^\circ$ so that the net force points vertically up (Wang 2004). Then the wing could return to the starting position with a zero angle of attack during the upstroke. Rather than tilting the horizontal stroke as Wang suggested, we created a theoretical stroke in the vertical plane. This stroke also has a net force that points vertically up during the downstroke, and a wing that returns to the starting position with a zero angle of attack during the upstroke. Assuming that the upstroke contributes almost no force, Wang estimated that the average $\overline{C_V}$ would be 0.99 for a complete stroke at $Re=150$. Our results indicate that $\overline{C_V}$ would be ~ 0.9 at $Re=150$. Our results are slightly lower than Wang's because our model does not assume zero force during the upstroke and the upstroke does contribute some negative C_V .

Bennet (1973) suggested that a faster downstroke velocity would enhance $\overline{C_V}$ produced by a drag-based mechanism. Observed insects to-date actually have downstrokes that are slower than their upstroke. Since little is known about the flapping kinematics of the smallest insects, we wanted to investigate the effectiveness of a drag-based stroke with faster downstrokes. Our results indicate that a faster downstroke does increase $\overline{C_V}$ and $\overline{C_V}/\overline{C_T}$ in a vertical stroke. The increase in performance with increasing downstroke velocity is dependent on Re . The magnitude of the effect decreases as Re decreases. At the Re of the smallest flying insects, a vertical stroke with the downstroke twice as fast as the upstroke actually slightly outperforms a lift-based horizontal stroke; however, the increase in performance is modest. Interestingly, *Encarsia formosa* has been observed to have a faster upstroke than downstroke with $\eta=0.75$ (Weis-Fogh 1973). Our results suggest that an insect performing a vertical stroke with $\eta=0.75$ would perform worse than insects with larger η .

Flexibility has been demonstrated to play an important role in drag reduction in a number of studies (Alben, Shelley et al. 2002; Miller and Peskin 2004; Miller and Peskin 2009; Miller,

Santhanakrishnan et al. 2012). Consequently, we expected that flexibility would play a role in wing performance. We compared the three stroke types using both a flexible and a rigid wing (Fig 22 and 23). There was little difference between the flexible and rigid wings for the lift-based horizontal stroke. However, $\overline{C_V}$ increased for the flexible wing case for the tilted and vertical strokes, and the $\overline{C_V}/\overline{C_T}$ increased for the flexible wing case for the tilted stroke. The greatest increase in $\overline{C_V}$ and $\overline{C_V}/\overline{C_T}$ was observed for the tilted stroke (Fig 23b). However, even with the increase in performance with added flexibility, the tilted and vertical stroke still had lower forces and $\overline{C_V}/\overline{C_T}$ than the horizontal stroke at Re pertinent to the smallest insects.

5. Conclusions

The results of our study suggest it is possible that a small insect could theoretically use a drag-based strategy to produce as much $\overline{C_V}$ as a lift-based strategy, although we are unaware of any insects that have a drag-based stroke at very low Re . It is important to point out that neither lift- nor drag-based weight support mechanisms are very efficient at $Re < 100$, and particularly at $Re < 20$, which is the range of the smallest flying insects. This may help explain the importance of additional flight strategies not included in this study, such as wing-wing interactions (Lighthill 1973; Weis-Fogh 1973; Maxworthy 1979; Ellington 1984; Ellington 1984; Spedding and Maxworthy 1986; Sun and Xin 2003; Lehmann, Sane et al. 2005; Miller and Peskin 2005; Sun and Yu 2006; Lehmann and Pick 2007; Miller and Peskin 2009) and bristled wings (Cheer and Koehl 1987; Sunada, Takashima et al. 2002).

This study only considers the vertical force that could be produced by tiny insects. We did not consider the advantages that either lift or drag based mechanisms might have for other components of flight. Previous computational work for larger insects has shown that it is easy to synthesize optimized computational models of wing strokes that exceed the performance of the biological stroke when the measurement of aerodynamic performance is defined in terms of force, power, or efficiency (Berman and Wang 2007; Nakata and Liu 2012; Zheng, Hedrick et al. 2013). However, the design of insect wing kinematics is the result of compromise among many factors, including stability, maneuverability, control, and wing strength. Vertical force alone cannot fully explain whether tiny insects would use lift or drag mechanisms. For example, at higher Re , stability increases as the stroke plane angle increases (Xu and Sun 2014). Additional studies into the maneuverability, stability and control of insects at low Re would be beneficial to understanding the flight strategies employed by these insects.

While this study was conducted using 2D cross sections of an insect wing, we expect that the 3D geometry of wings will play an important role in aerodynamic performance. In general, 2D studies fail to capture any effects from span-wise flow, and there can be differences in the separation of the LEV, especially at higher Re (Wang, Birch et al. 2004). The 2D study also fails to take into account that the flapping wings of insects are rotated about a wing base, rather than translated. Especially during stroke reversal with a tilted stroke plane, the vector normal to the wing surface does not typically point upward. This effect is more significant for insects with

418 larger wing stroke amplitudes. We only considered linear stroke planes; however, the wing tip
 419 of many insects actually trace more complicated patterns such as ovals, parabolas, or figure
 420 eights (Wang 2004). We also did not consider the effects of wing-wing interactions—it is widely
 421 believed that many tiny insects use clap and fling to enhance lift (Weis-Fogh 1973). Large
 422 forces are required to fling the wings apart at low Re (Miller and Peskin 2005); however, it is
 423 possible that bristles on the wing could reduce the force required to clap the wings together and
 424 fling the wings apart (Miller and Peskin 2009). The flight mechanisms employed by insects at
 425 $Re < 100$ requires further investigation.

426 **Acknowledgements**

427 This work was partially funded by the National Science Foundation (CAREER, DMS Math
 428 Biology), (CBET Fluid Dynamics 1151478) and (DMS Math Biology and CBET Fluid
 429 Dynamics 1022802) to LAM; and NSF awards DMS 1016554 and ACI 1047734 (to New York
 430 University School of Medicine) and NSF awards DMS 1460368 and ACI 1460334 (to the
 431 University of North Carolina at Chapel Hill) to BEG. This material is also based upon work
 432 supported by the NSF GRFP under Grant No. DGE-1144081 awarded to SKJ.

433 **List of Symbols**

Re	Reynolds number
ρ	density of air
μ	dynamic viscosity
c	chord length of wing
U	wing tip velocity
A_0	amplitude of translation
f	frequency
β	stroke plane angle
α	chord orientation relative to the stroke plane
α_0	mean angle of attack
B	amplitude of rotation
$\mathbf{x}$	Eulerian position (x, y)
$\mathbf{u}(\mathbf{x}, t)$	fluid velocity
$p(\mathbf{x}, t)$	pressure
$\mathbf{f}(\mathbf{x}, t)$	force per unit area
$\mathbf{F}(r, t)$	force per unit length
r	Lagrangian position
t	time
$\delta(\mathbf{x})$	two-dimensional delta function
$\mathbf{X}(r, t)$	Cartesian coordinates of the material point
U_{max}	maximum velocity of the wing
U_{rms}	root mean square of the velocity
F_V	vertical force

F_H	horizontal force
C_V	vertical force coefficient
C_H	horizontal force coefficient
$\overline{C_V}$	net vertical force (average over time)
$\overline{C_T}$	net total force (average over time)
k'_{beam}	dimensionless bending stiffness
$\hat{\kappa}$	curvature
$\hat{n}$	unit vector normal wing
T	tension
$\hat{r}$	unit tangent to the wing
η	ratio of downstroke to upstroke velocity
$T_{downstroke}$	time to complete downstroke
$T_{upstroke}$	time to complete upstroke
f_{avg}	average frequency

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Figures

Figure 1. (A) A cross section through the chord of the wing provides a simplified way to study insect wing aerodynamics in two dimensions. (B) Drag (F_D) is the component of force in the

563 direction of oncoming airflow relative to the motion of the wing, and lift (F_L) is the component
564 of force normal to oncoming airflow. Vertical force (F_V) is the component of force opposing
565 gravity, and horizontal force (F_H) is the component of force normal to gravity.

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Figure 2. Idealized wing kinematics (sections through the chord of the wing). The closed circle represents the leading edge of the wing, and each half-stroke is shown separately. The solid black arrows indicate the direction and relative magnitude of dimensionless drag (C_D) during each half-stroke, and the solid grey arrows indicate the direction and relative magnitude of dimensionless lift (C_L). The solid axes on the right indicate the net C_D and C_L during a complete stroke. The direction of dimensionless vertical (C_V) and dimensionless horizontal (C_H) force always face the same direction with respect to the global frame (dashed arrows). (a) A horizontal, lift-based stroke ($\alpha_0=90^\circ, \beta=0^\circ$) uses only C_L to produce C_V . (b) A vertical, drag-based stroke ($\alpha_0=45^\circ, \beta=90^\circ$) uses only C_D to produce C_V . (c) A tilted, hybrid stroke ($\alpha_0=60^\circ, \beta=62.8^\circ$) uses both C_L and C_D to produce C_V .

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601 Figure 3. Refinement study displaying C_V and C_H as functions of dimensionless time for the
602 horizontal stroke at (a) $Re=10$, (b) $Re=100$, and (c) $Re=200$. The legend denotes the mesh size of
603 the finest grid near the wing and regions of vorticity. Effective 512×512 grid discretization was
604 used for all other simulations with $Re \leq 100$, and 1024×1024 grid discretization was used for all
605 other simulations with $Re > 100$ in this paper.

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607 Figure 4. Comparison of IBAMR to an existing numerical method showing C_V and C_H as
608 functions of dimensionless time. We compared the lift-based stroke ($\alpha_0=90^\circ$, $\beta=0^\circ$, $A_0/c=2.5$,
609 $f=1$, and $B=\pi/4$) at $Re=150$. Overall, there is good agreement between our simulation and the
610 simulation described by Wang (28). Only the last two wing beats are shown.

Figure 5. Instantaneous C_V and C_H as functions of dimensionless time for the horizontal lift-based stroke at Re 1, 5, 10 and 100 ($\alpha_0=90^\circ$, $\beta=0^\circ$, $A_0/c=2.5$, $f=1$, and $B=\pi/4$). Only the last two wing beats are shown.

Figure 6. Instantaneous C_V and C_H as functions of time for the tilted hybrid stroke at Re 1, 5, 10 and 100 ($\alpha_0=60^\circ$, $\beta=62.8^\circ$, $A_0/c=2.5$, $f=1$, and $B=\pi/4$).

Figure 7. Instantaneous C_V and C_H as functions of time for the vertical drag-based stroke at Re 1, 5, 10 and 100 ($\alpha_0=45^\circ$, $\beta=90^\circ$, $A_0/c=2.5$, $f=1$, and $B=\pi/4$).

Figure 8. Vorticity plots of the horizontal stroke during the 4th wingbeat at (A) $Re=10$ and (B) $Re=100$, shown at (i) the beginning of downstroke, (ii) midway through downstroke, (iii) at the beginning of upstroke, and (iv) midway through upstroke. The vectors show the direction of flow and are scaled to the magnitude of the flow velocity. The colour map shows the vorticity of the fluid (min=-60 and max=60). Online version in colour (red, counter clockwise rotation; blue, clockwise rotation).

Figure 9. Vorticity plots of the tilted stroke during the 4th wingbeat at (A) $Re=10$ and (B) $Re=100$, shown at (i) the beginning of downstroke, (ii) midway through downstroke, (iii) at the beginning of upstroke, and (iv) midway through upstroke. The vectors show the direction of flow and are scaled to the magnitude of the flow velocity. The colour map shows the vorticity of the fluid (min=-60 and max=60). Online version in colour (red, counter clockwise rotation; blue, clockwise rotation).

Figure 10. Vorticity plots of the vertical stroke during the 4th wingbeat at (A) $Re=10$ and (B) $Re=100$, shown at (i) the beginning of downstroke, (ii) midway through downstroke, (iii) at the beginning of upstroke, and (iv) midway through upstroke. The vectors show the direction of flow and are scaled to the magnitude of the flow velocity. The colour map shows the vorticity of the fluid (min=-60 and max=60). Online version in colour (red, counter clockwise rotation; blue, clockwise rotation).

Figure 11. Net dimensionless vertical forces as functions of Re , shown for (a) all Re studied and (b) Re in the range of the smallest flying insects. The forces are averaged over the 3rd and 4th wing beats.

Figure 12. Net vertical force normalized by the total magnitude of force experienced by the wing ($\overline{C_V}/\overline{C_T}$) as a function of Re , shown for (a) all Re studied and (b) Re in the range of the smallest flying insects. The horizontal stroke has a higher $\overline{C_V}/\overline{C_T}$ for $Re > 5$.

Figure 13. Instantaneous C_V and C_H as functions of time for the vertical drag-based stroke with different ratios of downstroke and upstroke velocity (η) for (a) $Re=10$ and (b) $Re=100$.

Figure 14. Net dimensionless vertical forces as functions of Re for different ratios of downstroke velocity to upstroke velocity (η) shown for the vertical stroke at (a) all Re studied and (b) Re in the range of the smallest flying insects. Greater ratios produce larger $\overline{C_V}$. The symmetric ($\eta=1$) horizontal stroke is shown for reference as the dashed line.

Figure 15. $\overline{C_V}/\overline{C_T}$ as a function of Re for different ratios of downstroke velocity to upstroke velocity (η) shown for (a) all Re studied and (b) Re in the range of the smallest flying insects. Greater ratios have higher $\overline{C_V}/\overline{C_T}$. The symmetric ($\eta=1$) horizontal, lift-based stroke is shown for reference as the dashed line.

Figure 16. Vorticity plots of the vertical stroke with a downstroke that is twice as fast as the upstroke ($\eta=2$) during the 4th wingbeat at (A) $Re=10$ and (B) $Re=100$, shown at (i) the beginning of downstroke, (ii) midway through downstroke, (iii) at the beginning of upstroke, and (iv) midway through upstroke. The vectors show the direction of flow and are scaled to the magnitude of the flow velocity. The colour map shows the vorticity of the fluid (min=-60 and max=60). Online version in colour (red, counter clockwise rotation; blue, clockwise rotation).

Figure 17. Plots of the configuration of a rigid wing (gray line) and a flexible wing (black line) engaged in the vertical stroke at $Re=10$, shown at (A) the beginning of downstroke, (B) midway through downstroke, (C) at the beginning of upstroke, and (D) midway through upstroke. The greatest deformation among all of the strokes analyzed occurs during the middle of downstroke for the vertical stroke.

Figure 18. Vorticity plots of the horizontal stroke with a flexible wing during the 4th wingbeat at (A) $Re=10$ and (B) $Re=100$, shown at (i) the beginning of downstroke, (ii) midway through downstroke, (iii) at the beginning of upstroke, and (iv) midway through upstroke. The vectors show the direction of flow and are scaled to the magnitude of the flow velocity. The colour map shows the vorticity of the fluid (min=-60 and max=60). Online version in colour (red, counter clockwise rotation; blue, clockwise rotation).

Figure 19. Vorticity plots of the tilted stroke with a flexible wing during the 4th wingbeat at (A) $Re=10$ and (B) $Re=100$, shown at (i) the beginning of downstroke, (ii) midway through downstroke, (iii) at the beginning of upstroke, and (iv) midway through upstroke. The vectors show the direction of flow and are scaled to the magnitude of the flow velocity. The colour map shows the vorticity of the fluid (min=-60 and max=60). Online version in colour (red, counter clockwise rotation; blue, clockwise rotation).

708 Figure 20. Vorticity plots of the vertical stroke with a flexible wing during the 4th wingbeat at
709 (A) $Re=10$ and (B) $Re=100$, shown at (i) the beginning of downstroke, (ii) midway through
710 downstroke, (iii) at the beginning of upstroke, and (iv) midway through upstroke. The vectors
711 show the direction of flow and are scaled to the magnitude of the flow velocity. The colour map
712 shows the vorticity of the fluid (min=-60 and max=60). Online version in colour (red, counter
713 clockwise rotation; blue, clockwise rotation).

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Figure 21. Instantaneous C_V and C_H as functions of dimensionless time for flexible wing and rigid wings at (i) $Re=10$ and (ii) $Re=100$, shown for (a) the horizontal stroke, (b) the titled stroke, and (c) the vertical stroke.

Figure 22. Net dimensionless vertical forces as functions of Re for the flexible and rigid wings, shown for (a) the horizontal stroke, (b) the titled stroke, and (c) the vertical stroke.

Figure 23. $\overline{C_V}/\overline{C_T}$ as functions of Re for the flexible and rigid wing, shown for (a) the horizontal stroke, (b) the titled stroke, and (c) the vertical stroke.

736 **Table 1.** Ratio of downstroke velocity to upstroke velocity.

Insect	Velocity Ratio (η)
<i>Encarsia formosa</i> (Weis-Fogh 1973)	0.75
Thrips (Santhanakrishnan, Robinson et al. 2014)	0.88
Fruit fly (Zanker 1990)	0.6
Honeybee (Osborne 1951)	0.77
House fly (Osborne 1951)	0.67

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738 **Table 2.** Numerical parameters.

Dimensionless parameter	Value
Chord length (c)	0.1
Domain length (L)	2
Finest Grid Refinement (Re<100)	512X512
Finest Grid Refinement (Re>100)	1024X1024
Number of refinement levels	4
Refinement ratio	1:4
Time step (dt)	1.0e-6
Final simulation time	4
Spatial step size (dx)	L/Finest Grid Refinement
Target stiffness (k'_{targ})	64
Spring stiffness (k'_{spring})	638
Beam stiffness (k'_{beam})	31

739
740 **Table 3.** Average percent difference in forces over 2 wing strokes between different grid
741 refinements at three different Re .

		% Difference	
Grids		C_V	C_H
$Re=200$	256X256 vs. 512X512	19.9	19.4
	512X512 vs. 1024X1024	9.6	7.5
	1024X1024 vs. 2048X2048	4.4	3.4
$Re=100$	256X256 vs. 512X512	15.1	13.4
	512X512 vs. 1024X1024	5	4.1
	1024X1024 vs. 2048X2048	2.9	2.6
$Re=10$	256X256 vs. 512X512	6.3	10.8
	512X512 vs. 1024X1024	3	3.1
	1024X1024 vs. 2048X2048	1.2	1.8

743 **Table 4.** Average percent difference in forces over 2 wing strokes between different Re for the
 744 horizontal stroke on a 512X512 grid.

	% Difference	
	C_V	C_H
$Re=100$ vs. $Re=10$	94	53
$Re=10$ vs. $Re=5$	34	25
$Re=5$ vs. $Re=1$	67	55

745