Journal of Theoretical Biology 384 (2015) 105–120

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

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

S.K. Jones[a,*], R. Laurenza[a], T.L. Hedrick[b], B.E. Griffith[a], L.A. Miller[a,b]

[a] Department of Mathematics, University of North Carolina, Chapel Hill, NC 27599, USA
[b] Department of Biology, University of North Carolina, Chapel Hill, NC 27599, USA

HIGHLIGHTS

- Both drag and lift have been suggested as mechanisms used by tiny insects.
- We used CFD to compare the force generated by lift- and drag-based hovering.
- We compared three idealized hovering kinematics.
- At the *Re* of tiny insects, there is little difference between the two strategies.

ARTICLE INFO

Article history:
Received 17 October 2014
Received in revised form
3 June 2015
Accepted 31 July 2015
Available online 20 August 2015

Keywords:
Insect flight
Computational fluid dynamics
Immersed boundary method
Biomechanics

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.

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 et al., 1990; Crespi 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 et al., 2002; Miller and Peskin, 2004, 2005, 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 200 Hz (Santhanakrishnan et al., 2014) and possibly as high as 400 Hz (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

* Corresponding author. Tel.: +1 919 843 4557.
E-mail address: skjohnsn@email.unc.edu (S.K. Jones).

http://dx.doi.org/10.1016/j.jtbi.2015.07.035
0022-5193/

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
$\mathrm{p}(\mathbf{x},t)$	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 to the wing
T	tension
$\hat{\tau}$	unit vector 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

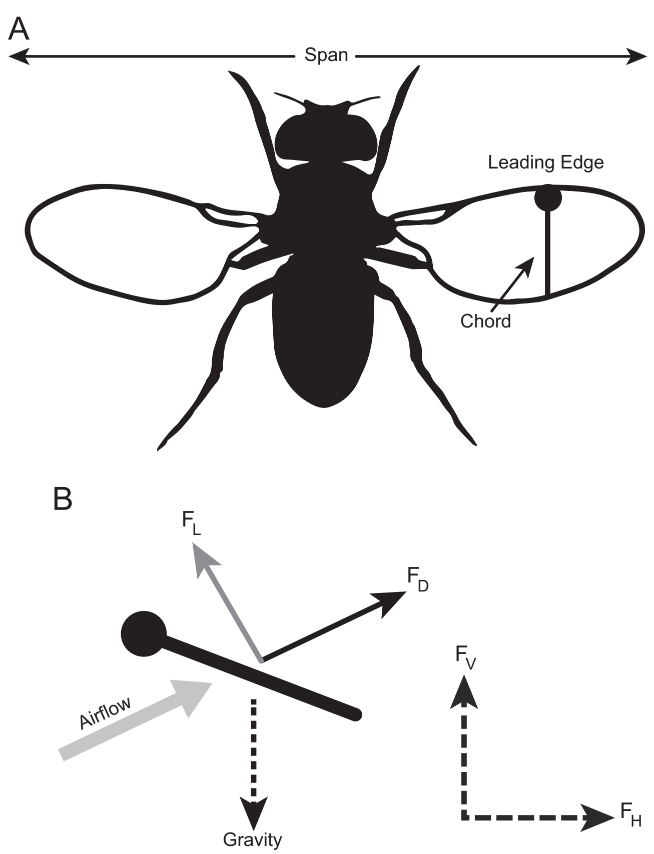

Fig. 1. (A) A cross section through the chord of the wing provides a simplified way to study insect wing aerodynamics in two dimensions. (B) Drag (F_D) is the component of force in the direction of oncoming airflow relative to the motion of the wing, and lift (F_L) is the component of force normal to oncoming airflow. Vertical force (F_V) is the component of force opposing gravity, and horizontal force (F_H) is the component of force normal to gravity.

(Fig. 1a)

$$Re = \frac{\rho U c}{\mu}, \tag{1}$$

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 et al., 1999) and *Manduca sexta* (Usherwood and Ellington, 2002; Hedrick 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, 1984a), 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, whereas F_H is normal to gravity. Unlike lift and drag, F_V and F_H always face the same direction with respect to the global frame. We will adhere to these definitions of lift, drag, F_V and F_H as we investigate force production and flight aerodynamics of the smallest insects.

A lift-based strategy for small insect flight became widely accepted following Weis-Fogh's influential 1973 paper that described clap and fling (Weis-Fogh, 1973). Subsequently, a combination of work supported the idea that insects increase the lift