Here, we present a detailed analysis of the take-off mechanics in droneflies performing voluntary take-offs. Wing and body kinematics of the insects during take-off were measured using high-speed video techniques. Based on the measured data, the inertia force acting on the insect was computed and the aerodynamic force of the wings was calculated by the method of computational fluid dynamics. Subtracting the aerodynamic force and the weight from the inertia force gave the leg force. In take-off, a dronefly increases its stroke amplitude gradually in the first 10–14 wingbeats and becomes airborne at about the 12th wingbeat. The aerodynamic force increases monotonously from zero to a value a little larger than its weight, and the leg force decreases monotonously from a value equal to its weight to zero, showing that the droneflies do not jump and only use aerodynamic force of flapping wings to lift themselves into the air. Compared with take-offs in insects in previous studies, in which a very large force (5–10 times of the weight) generated either by jumping legs (locusts, milkweed bugs and fruit flies) or by the ‘fling’ mechanism of the wing pair (butterflies) is used in a short time, the take-off in the droneflies is relatively slow but smoother.

1. Introduction

Take-off is the first manoeuvre in the entire flight envelope, and so plays an important role in the biology of flying insects. Although in previous works, there have been many photographs and short descriptions of flight initiation of a variety of insects, detailed analysis of unrestrained take-off flight has been done for only a few insects [1–6]. Pond [1] studied the take-off in the locust, *Schistocerca gregaria*, and showed that the locusts first jump into the air, and then start wing flapping to fly, and there is a 33 ms delay between the metathoracic tarsi leaving the ground and the start of visible wing movement. Govind & Dandy [2] analysed the series of events at the start and cessation of flight in the milkweed bug, *Oncopeltus*, and showed that the take-off jump (executed by a complex of trochanteral depressor muscles of the meso- and metathoracic legs) occurs after wing flapping has started for about two wingbeats. Trimachi & Schneiderman [3] showed that the fruit fly, *Drosophila melanogaster*, performs two types of flight initiation: one is a stereotyped escape take-off triggered by strong visual stimuli, and the other is a more variable ‘voluntary’ take-off performed without any overt stimulus. Card & Dickinson [4] and Fontaine *et al.* [5] captured detailed wing, body and leg motions of *D. melanogaster* performing the two types of take-off. In an escape take-off, the fly jumps into the air with wings in the closed position and opens the wings only after they are fully airborne. In a voluntary take-off, the fly first opens its wing and then starts the jump; the motion of the legs and wings are coordinated so that at the start of the jump, the wings elevate further but then quickly start the first downstroke as the legs complete their extension and the insect becomes airborne. Sunada *et al.* [6] measured the wing and body kinematics of a butterfly in take-off flight using a high-speed video camera and computed the aerodynamic force of the flapping wings using a vortex method. They found that the lift-off is caused by a large aerodynamic force generated by the wings in their first half of the first downstroke and that the interference effect between a pair of wings with the small initial opening angle is responsible...
for the large aerodynamic force (this high lift mechanism of fast opening a wing-pair is referred to as the ‘fling’ mechanism [7]). Insects in the above studies [1–6] lift themselves into the air using large force generated either by jumping legs (locusts, milkweed bugs and fruit flies) or by wings using the ‘fling’ mechanism (butterflies). The take-off is relatively fast. For example, for fruit flies at voluntary take-off, the insects become airborne in less than half a wingbeat, and the maximum vertical acceleration is around 6 g (where g is the gravitational acceleration), i.e. the maximum vertical force generated by the jumping legs is six times as large as the weight of the insect (at escape take-off, the acceleration is even larger, around 12 g) [4]; for the butterfly take-off, the insect becomes airborne in less than a quarter of a wingbeat and the maximum vertical acceleration is about 10 g [6]. Our group conducted experimental studies on the hovering flight of droneflies and hoverflies [8,9], and manoeuvre flight of droneflies [10]. During some of the tests, take-off flights of the insects were observed. We noted that droneflies and hoverflies perform a much slower voluntary take-off. Little is known about the kinematics and dynamics of this type of take-off.

In this work, we examine the voluntary take-offs of droneflies (Eristalis tenax) which, as aforementioned, is relatively slow compared with the insects considered in the above studies [1–6]. We measure the body motion and the flapping motion of the wings during the flight initiation of the insects, using three-dimensional high-speed video techniques, and we also measure the morphological parameters of the insects. From the measured body acceleration, the inertia force acting on the insect can be estimated. We use a computational fluid dynamics (CFD) method to compute the aerodynamic force of the wings. Subtracting the aerodynamic force and the weight of the insect from the inertia force gives an estimate of the leg force. With the time histories of these forces known, the contributions of the wings and the legs and the transition from leg force to wing force during take-off can be determined.

2. Material and methods

2.1. Animals

We netted droneflies of the species E. tenax in a suburb of Beijing in June 2011. The flies were released into a relatively large enclosure (1.5 × 1.5 × 1.5 m) in the laboratory, the walls of which were made of mesh screening. Some of the flies flew around vigorously, whereas some remained on the wall. Only the most actively flying individuals were selected for the experiments. All experiments were conducted on the same day of capture.

2.2. Three-dimensional high-speed filming

We filmed voluntary take-offs of the droneflies using three orthogonally aligned synchronized high-speed cameras (MotionXtra HG-LE, Redlake MASD, Inc., San Diego, CA, USA; 5000 frames s⁻¹, shutter speed 50 μs, resolution 512 × 320 pixels) mounted on an optical table. The flies took off from a 3 × 3 cm² platform made of translucent glass. The platform was surrounded by water and was inside and at the bottom of a 30 × 30 × 30 cm³ flight chamber (also made of translucent glass). We backlit each camera view using a 50 W integrated red light emitting diode (LED; luminous flux, 4000 lm; wavelength, 632 nm, which is beyond the visible range of E. tenax [11,12]). The light was made uniform by two lenses. We used integrated LEDs as the light source because they produced much less heat than cine lights at the elevated light levels required for high-speed filming. We manually triggered the synchronized cameras when the insect was observed to take-off in the approximately 5 × 5 × 5 cm³ cubic zone above the platform, which represented the intersecting field of views of the three cameras.

2.3. Measurement of wing and body kinematics and morphological parameters

The method we used to extract the three-dimensional body and wing kinematics from the filmed data was the same as that used by Liu et al. and others [8,9,13] (for the recent development of the measuring methods, see [14–16]). The method had been described in detail by Mou et al. [9] and only an outline of it is given here. The body and wings were represented by models. The model of a wing was the outline of the wing obtained by scanning the cut-off wing (figure 1), and that of the body is the line connecting the head and end of abdomen and the line connecting the two wing hinges (figure 2). An interactive graphic user interface was developed using MATLAB (MATLAB v. 7.1, The Mathworks, Inc., Natick, MA, USA) to extract the three-dimensional body and wing positions from the frames recorded by the three cameras (an example of the frames is shown in figure 2). The positions and orientations of the models of the body and wings were adjusted until the best overlap between a model image and the displayed frame was achieved in three views (the fitting process was done manually).

At this point, the positions and orientations of these models were taken as the positions and orientations of the body and the wings. The specific fitting process at a time instant, say at time $tn$, is as following. Suppose that at last instant, $tn−1 = tn−Δt$ ($Δt$ is the time interval between two sequential frames and is 1/5000 s), the models of the body and wings were matched with the pictures of the body and wings (figure 2a). At time $tn$, the pictures of the body and the wings would be moved a little relative to the body and wings models at time $tn−1$ (figure 2b). With a few adjustments, the body and wings models at time $tn−1$ can be made to match the pictures of the body and the wings at time $tn$, as shown in figure 2c. Analysis by Mou et al. [9] showed that with this method, errors in positional angle and elevation angle of the wing were within 3° and errors in pitch angle (or angle of attack) were within 4° [9].

Figure 1. Wing model; $R$, wing length; $c$, local chord length of wing. (Online version in colour.)
The method we used to measure the morphological parameters was also the same as that used by Mou et al. [9] and it is briefly described here. The insects were killed with ethyl acetate vapour after filming. The total mass \( m \) was measured to an accuracy \( \pm 0.01 \) mg. The wings were then cut from the body and the mass of the wingless body was measured. The wing mass \( m_{wg} \) was determined by the difference between the total mass and the mass of wingless body. Immediately after the wings were cut from the body, the shape of one of them was scanned using a scanner (HP scanjet 4370; resolution 3600 × 3600 d.p.i.). A sample of the scanned picture of a wing is shown in figure 1. Using the scanned picture, wing length \( R \) (the distance between the wing base and the wing tip) and local wing chord length were measured to an accuracy greater than \( \pm 0.5\% \). Parameters including wing area, mean chord length and radius of second moment of wing area, etc. were computed using the measured wing shape. The wingless body was scanned from two perpendicular directions, the dorsoventral view and the lateral view (figure 3). A long axis of body was drawn on the lateral view, approximately cutting the body into dorsal and ventral halves (figure 3). The body was divided into \( n \) strips (typically 100) perpendicular to this axis. The cross-section of the body was taken as an ellipse and uniform density was assumed for the body. Thus, the centre of mass (COM) of each strip could be determined. The COM of the body was then determined from those of the \( n \) strips. Body length \( l_b \) and the distance between the wing roots \( l_r \) were measured from the dorsal views; the distance between the wing-root axis and the COM \( l_1 \) and the distance between the wing-base axis and the long axis of the body \( h_1 \) were measured from the lateral view (figure 3).

2.4. Determination of the total force acting on the insect and the leg force

Based on the measured position data of the body COM and the mass of the insect, the total force acting on the insect could be calculated. Taking the first and second derivatives of the smoothed position data gave the velocity and acceleration...
of the COM, respectively. Multiplying the COM acceleration by the mass of the insect gave the inertia force acting on the insect.

The inertia force acting on the insect was equal to the summation of the aerodynamic force on the insect, the leg force and the weight. The leg force was obtained by subtracting the aerodynamic force (see below for its determination) and the insect weight from the inertia force.

2.5. Computation of aerodynamic force

The aerodynamic force acting on the insect was computed by numerically solving the Navier–Stokes equations. In the solution, moving overset grids were used because there was relative motion between the left and right wings and between the insect and the ground plane. The numerical method was the same as that used by Sun et al. in several previous studies [17–19] and a description of it is given in the electronic supplementary material; the computational grids and grid resolution tests are also given there.

3. Results and discussion

Five voluntary take-offs performed by three droneflies at the zone of the intersecting field of view of the three cameras were filmed. The three droneflies were denoted as DF1, DF2 and DF3, respectively. Two take-offs were performed by DF1, two by DF2 and one by DF3. Each take-off flight sequence comprised about 25 stroke cycles and there were 30 frames per stroke cycle. For the five sequences, 4000 frames were analysed. Because the amount of frames is large for each flight sequence and because, as will be seen below, the interindividuation variance is very small, we believe that there is no need to enlarge the data volume. A sample of the original video sequences for DF1 is given in the electronic supplementary material, movie S1, and a movie showing the wing and body models superimposed on to the original footage is also given in the electronic supplementary material, movie S2.

To describe the wing kinematics of the insects, we follow the method given by Ellington [20]. For the dronefly take-off, after the first 8–10 strokes, the wingbeat amplitude and frequency become approximately constant (see figure 8).

The aerodynamic force acting on the insect was equal to the summation of the aerodynamic force on the insect, the leg force and the weight. The leg force was obtained by subtracting the aerodynamic force (see below for its determination) and the insect weight from the inertia force.

To describe the body kinematics, we follow the convention from dynamics of flight described by Etkin & Reid [21]. We define two frames of reference (figure 5): the
Table 1. Morphological parameters of the droneflies. DF1, DF2 and DF3, droneflies 1, 2 and 3, respectively; m, mass of the insect; \( m_{wg} \), mass of one wing; R, wing length; S, area of one wing; \( l_b \), body length; \( l_r \), distance from wing-root axis to long-axis of body; \( l_l \), distance from wing-root axis to body centre of mass; \( l_a \), distance from anterior end of body to centre of mass; \( l_{Rj} \), distance between two wing-roots; \( r_j \), radius of second moment of wing area.

<table>
<thead>
<tr>
<th>individual</th>
<th>m (mg)</th>
<th>( m_{wg} ) (mg)</th>
<th>R (mm)</th>
<th>S (mm²)</th>
<th>( l_b ) (mm)</th>
<th>( h_1/l_b )</th>
<th>( l_1/l_b )</th>
<th>( l_2/l_b )</th>
<th>( l_3/l_b )</th>
<th>( r_j/R )</th>
</tr>
</thead>
<tbody>
<tr>
<td>DF1</td>
<td>116.11</td>
<td>0.97</td>
<td>11.88</td>
<td>33.51</td>
<td>14.82</td>
<td>0.095</td>
<td>0.117</td>
<td>0.469</td>
<td>0.312</td>
<td>0.562</td>
</tr>
<tr>
<td>DF2</td>
<td>135.84</td>
<td>0.80</td>
<td>11.60</td>
<td>35.47</td>
<td>14.69</td>
<td>0.058</td>
<td>0.142</td>
<td>0.475</td>
<td>0.373</td>
<td>0.546</td>
</tr>
<tr>
<td>DF3</td>
<td>100.82</td>
<td>0.96</td>
<td>12.57</td>
<td>38.21</td>
<td>15.21</td>
<td>0.101</td>
<td>0.144</td>
<td>0.478</td>
<td>0.302</td>
<td>0.557</td>
</tr>
</tbody>
</table>

Earth-fixed frame \((x_E, y_E, z_E)\), where the \( x_E \) and \( y_E \) axes are horizontal and the \( z_E \) axis is vertical, pointing downward; and the insect’s body-fixed frame \((x_b, y_b, z_b)\), where the origin is at the COM of the insect’s body, the \( x_b \) axis is along the body, pointing from tail to head, and the \( y_b \) axis points to the right side of the body. The position of the COM of the insect’s body is given by its displacements in \( x_E, y_E \) and \( z_E \) directions, denoted as \( \Delta x_E, \Delta y_E \) and \( \Delta z_E \), respectively. The orientation of the insect’s body is given by the three Euler angles (see [21]), denoted as \( \phi_b, \theta_b \) and \( \phi_h \) (they are referred to as heading, pitch and roll angles of the body, respectively, in this study).

3.1. Morphological parameters

The measured morphological parameters of the insects are given in table 1. Parameters in the table include the total mass of an insect \( m \), mass of one wing \( m_{wg} \), the wing length \( R \), area of one wing \( S \), the second moment of wing area \( r_j \), body length \( l_b \), distance between the two wing roots \( l_r \), distance between the wing-base axis and the COM \( l_l \), distance from the anterior end of the body to the COM \( l_a \) and distance between the wing-base axis and the long axis of the body \( l_h \).

3.2. Start of flight

Figure 6 shows the complete sequences of a dronefly (DF1) starting flight (in this paper, the time when the COM of the insect body starts to rise is taken as zero). First, the insect raises its wings to a position of \( \phi \approx 40^\circ \) (figure 6a,b); the wing raising is relatively slow, taking about 10 ms. Then the insect starts its wing flapping (figure 6b); at first, the stroke amplitude is relatively small but it increases with time (figure 7). In the first six strokes (figure 6b–m), the body does not have observable motion. From about the 7th stroke to the 12th stroke (figure 6n–z), the body is observed to slowly rise, but some of the legs are still in contact with the platform. After the 13th stroke (figure 6z–z(iii)), all the legs leave the platform and the insect becomes airborne. The above take-off sequences can be viewed more clearly in the electronic supplemental material, movie S1.

Take-offs of other droneflies recorded in this study are similar.

3.3. Wing and body kinematics

Figure 7 shows the measured angles of wing flapping as functions of time for the left and the right wings of DF1 (data for DF2 and DF3 and for the second take-off flight of DF1 are similar). Let \( \Phi \) and \( \phi \) denote stroke amplitude and mean stroke angle, respectively; they are defined by \( \Phi = (\phi_{\text{max}} + \phi_{\text{min}})/2 \) and \( \phi = \phi_{\text{max}} - \phi_{\text{min}} \) where \( \phi_{\text{max}} \) and \( \phi_{\text{min}} \) are the maximum and minimum values of \( \phi \), respectively (see Ref. [20]). From data in figure 7, wingbeat frequency \( n \), \( \Phi \) and \( \phi \) can be determined; they are shown in figure 8 (results for other insects are also shown in the figure). At the beginning, the stroke amplitude (figure 8b) is relatively small (about 45°) and it increases with time. It reaches its maximum values (about 120°) shortly before the insect is airborne and decreases a little (to about 100°) after the insect is airborne (figure 8b). The mean stroke angle is approximately constant (figure 8c), and the wingbeat frequency changes a little in the first 2–5 strokes (figure 8d).

For the take-offs, the separating times range from 37 to 42 ms (figure 8d), and the number of wingbeats between \( t = 0 \) and the separating times are about 7 (figure 8b,d), showing remarkable consistency across the trials. A possible explanation for this is as follows. As seen from figure 8a, for each insect the wingbeat frequency is approximately constant when \( t > 0 \).

Thus the mean lift produced in a wingbeat can be written as

\[
\left( \frac{\Phi_{l_1}}{\Phi} \right)^2 mg, \tag{3.1}
\]

where \( \Phi_{l_1} \) denotes the stroke amplitude at hovering flight. The vertical acceleration of the insect is

\[
\ddot{z}_b = \left( \frac{\Phi_{l_1}}{\Phi} \right)^2 mgm^{-1}, \tag{3.2}
\]

From the data given in figure 8b, it can be shown that \( (\Phi_{l_1}/\Phi) \) changes little among the insects. Therefore, the vertical acceleration is approximately the same for the insects, explaining why the insects use about the same number of wingbeats to lift themselves into the air.

Figure 9a,b shows the measured displacement of the COM and the orientation of the body, respectively, as functions of time for DF1 (data for DF2 and DF3 and for the second take-off flight of DF1 are similar). The measured data were forward–backward filtered using the third-order low-pass Butterworth filter with the cut-off frequency at 30 Hz (the smoothed data are also shown in the figure 9a,b). It is seen that during the take-off, the lateral displacement, \( \Delta y_b \), and the heading and roll angles, \( \phi_h \) and \( \phi_r \), are close to zero, i.e. the insect mainly has longitudinal motion during the take-off. Taking the first and second derivatives of the smoothed data of \( \Delta y_b, \Delta \phi_h \) and \( \phi_h \) gave the velocity and acceleration of the COM and the pitch angular velocity and angular acceleration of the body; the results are shown in figure 10. It is seen that during take-off, DF1 mainly has an
upward motion (figures 9a and 10a), and the pitch angle of its body increases from 19.5°, when it is still on the ground, to 35.7°, when it is airborne (figure 9b). The vertical acceleration of the COM has its maximum value just before the insect is airborne (figure 10b) and the magnitude of the maximum value is about 4 m s\(^{-2}\), much smaller than that of a fruit fly in voluntary take-off (about 60 m s\(^{-2}\) \cite{4}). The maximum angular velocity of the body during take-off, which can be taken as an indication of the smoothness of the take-off \cite{4}, is 424 deg s\(^{-1}\), also much smaller than that of a fruit fly in voluntary take-off (about 2370 deg s\(^{-1}\) \cite{4}).

The corresponding results for the take-offs of other droneflies and for the second take-off of DF1 are similar, except that there are quantitative differences in the maximum
acceleration, maximum angular velocity of body and take-off angles. Table 2 gives the maximum acceleration and the maximum angular velocity of all take-offs of the droneflies. For all the take-offs, the maximum acceleration is less than 7.8 m s\(^{-2}\) and the maximum angular velocity is less than 600 deg s\(^{-1}\). Figure 11 shows the vertical displacement versus horizontal displacement of the body COM for all the take-offs of droneflies, which gives the take-off angles. The take-off angles are varied ranging from 26.0° to 67.3° and the mean take-off angle is approximately 45°.

The above data clearly show that interindividual variance in voluntary take-offs of the droneflies is rather low.

### 3.4. The total force, aerodynamic force and leg force

The inertia force acting on an insect was obtained by multiplying the COM acceleration (figure 10b) by the mass of the insect (table 1). The vertical and horizontal components of the inertia force are denoted by \(V_i\) and \(H_i\), respectively. The aerodynamic force produced by the flapping wings was computed by the CFD method described above, using the measured wing and body kinematics. As it was the wingbeat-cycle means of the aerodynamic force that affected the gross motion of the insect, we averaged the computed aerodynamic force in each wingbeat cycle. The vertical and horizontal components of the wingbeat-cycle-average aerodynamic force are denoted by \(V_a\) and \(H_a\), respectively. The leg force was estimated as follows:

\[
V_i = V_a - mg + V_{\text{leg}} \tag{3.3}
\]

and

\[
H_i = H_a + H_{\text{leg}} \tag{3.4}
\]

where \(V_{\text{leg}}\) and \(H_{\text{leg}}\) are the vertical and horizontal components of the leg force, respectively. The above equations give the leg-force components as:

\[
\frac{V_{\text{leg}}}{mg} = \left( \frac{V_i}{mg + 1} \right) - \frac{V_a}{mg} \tag{3.5}
\]

\[
\frac{H_{\text{leg}}}{mg} = \frac{H_i}{mg} - \frac{H_a}{mg} \tag{3.6}
\]

The time histories of \((V_i/\text{mg} + 1)\), \(V_a/\text{mg}\) and \(V_{\text{leg}}/\text{mg}\) of the insects are shown in figure 12 and those of \(H_i/\text{mg}\), \(H_a/\text{mg}\) and \(H_{\text{leg}}/\text{mg}\) are shown in figure 13.
As an example, let us discuss the results of DF2. As seen in figures 8b and 12c, before \( t/C25 \sim 20 \) ms, the wings have not started to flap and the body does not move, and the vertical aerodynamic force \( V_a \) and inertia force \( V_i \) are zero, hence the vertical leg force \( V_{\text{leg}} \) is equal to the weight of the insect \( mg \). At \( t/C25 \sim 40 \) ms, the wings start to flap and from \( t/C25 \sim 40 \) ms to \( t/C25 \sim 60 \) ms, the flapping amplitude increases with time (figure 8b). In this period, \( V_a \) increases with time, \( V_i \) also increases with time but only slightly and \( V_{\text{leg}} \) decreases with time (figure 12c). At \( t/C25 \sim 60 \) ms, \( V_a \) is approximately equal to \( V_i \) and \( V_{\text{leg}} \) decreases to zero (figure 12c), and the insect becomes airborne. For the second take-off of drone-fly DF2 (figure 12d) and the take-offs of other droneflies (figure 12a,b,c), the \( V_a, V_i \) and \( V_{\text{leg}} \) results are similar. As for

**Table 2.** Maximum acceleration of COM and angular velocity of body in each take-off (numbers in parentheses are the vertical and horizontal components of the maximum acceleration, respectively).

<table>
<thead>
<tr>
<th>take-off</th>
<th>max. acceleration ( (\text{m s}^{-2}) )</th>
<th>max. angular velocity ( (\text{deg s}^{-1}) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>DF1</td>
<td>4.18 (3.93, 1.42)</td>
<td>424</td>
</tr>
<tr>
<td>DF1a</td>
<td>5.45 (1.09, 5.34)</td>
<td>601</td>
</tr>
<tr>
<td>DF2</td>
<td>4.75 (2.84, 3.80)</td>
<td>337</td>
</tr>
<tr>
<td>DF2a</td>
<td>6.68 (2.75, 6.09)</td>
<td>178</td>
</tr>
<tr>
<td>DF3</td>
<td>7.73 (0.28, 7.72)</td>
<td>300</td>
</tr>
</tbody>
</table>
the horizontal components of the forces (figure 13), \(H_a\) and \(H_l\) are not very different, and the horizontal component of the leg force, \(H_{step}\), is small.

In summary, in take-off, a dronefly increases its stroke amplitude gradually in the first 10–14 wingbeats (the period of wingbeat is about 5.8 ms) and becomes airborne at about the 12th wingbeat. During this period, its aerodynamic force increases consistently from zero to a value a little larger than its weight, and its leg force decreases consistently from a value equal to the weight to zero, indicating that the dronefly does not jump and only uses aerodynamic force of the flapping wings to lift itself into the air. This is similar to a helicopter taking off: the aerodynamic force of the rotary wing increases monotonously from zero to a value larger than its weight, and the force on the carriage decreases monotonously from a value equal to its weight to zero.

### 3.5. Ground effect at take-off

When an animal or vehicle flies or swims near a substrate, the flow around the animal or vehicle could be different from that in the free air (or water) owing to the presence of the substrate (the substrate acting as a boundary). This effect is referred to as ground effect [22]. It has been shown that ground effect increases lift in birds and fishes flying or swimming at constant speed near a substrate [22]. Whether or not the ground effect plays any role in the take-off of the droneflies is unknown. In the above aerodynamic force computations, the ground plane was included. Here, we make more computations in which the ground plane is removed, and investigate the ground-effect problem by comparing the aerodynamic forces in the cases with and without the ground plane. Figure 14 shows the time histories of the vertical and horizontal components of the aerodynamic force of DF1 in cases with and without the ground plane. The aerodynamic force components in the case with the ground plane are almost identical to their counterparts in the case without the ground plane, showing that during take-off, ground effect on the aerodynamic force generation is negligibly small (the same is true for the take-offs of DF2 and DF3 and for the second take-off of DF1).

Engineers investigated ground effect on the aerodynamic performance of helicopter rotors, using the image of vortex wake to simulate the ground plane and the following have been shown [23]. At hovering flight, ground effect is significant when the height above ground \(h\) is small, but it decreases rapidly with the height above ground: at \(h = 0.5R\) (here, \(R\) denotes the rotor radius) ground effect is rather large, at \(h = 1.0R\) it becomes small, and when \(h > 2.0R\) it is negligible. At a fixed height above ground, ground effect decreases quickly with forward velocity, because the wake is swept backward rather than being directed at the ground. For the take-off of the droneflies, in the first 12 wingbeats or so \((t \approx 34 \text{ to } 38 \text{ ms})\), although the height above ground is small \((h = 0.5 \text{ to } 1.0R)\), the stroke plane is inclined forward (figure 6b–2) and the wake is not directed at the ground. This may explain the small ground effect in this period. In the later time \((t > 38 \text{ ms})\), the insect lifts above ground (figure 6z–2(vii)), and the height above ground becomes larger than 1.0R and keeps increasing; furthermore, the insect has a forward velocity-component during the lift-off. This may explain the small ground effect at \(t > 38 \text{ ms}\).

### 3.6. Comparison with take-offs in insects in previous studies

The behavioural sequences at unrestrained take-offs in several other species of insects (locust, \(S. \ gregaria\); milkweed bug, \(Oncopeltus\); fruit fly, \(D. \ melanogaster\) and butterfly, \(P. \ melete\)) were analysed by high-speed photography [1–6]. In addition, acceleration of COM and angular velocity of the body in voluntary take-offs in the fruit flies [4] and a butterfly [6] were measured, and the aerodynamic force generated by the wings in the butterfly was computed [6]. It is of interest to compare the take-offs of the droneflies analysed in this study with that of these insects.

Locusts, milkweed bugs and fruit flies take off using force generated by jumping legs [1,2,4], while droneflies do not jump during take-off and they lift themselves into the air using the aerodynamic force generated by flapping wings. The butterfly is similar to the droneflies in that it too only uses the aerodynamic force of flapping wings to take off. However, there is a major difference: the butterfly takes off using a short-time (impulsive) large force produced by the ‘fling’ mechanism; while the dronefly slowly increases its wingbeat amplitude and uses the gradually increasing aerodynamic force to take-off. The first downstroke (the ‘fling’) of the butterfly has an amplitude of about 160° [6]; while the amplitude of first downstroke of the dronefly is much smaller, only about 45° (figure 8).

Both the locusts, milkweed bugs and fruit flies, which take off by jumping, and the butterfly, which take-off by the ‘fling’ mechanism of wing-pair, have relatively fast take-off. For example, for the fruit fly, it takes less than half a wingbeat to become airborne [4] and for the butterfly, it takes a quarter of a wingbeat to become airborne [6]. However, for the droneflies, the take-off is relatively slow; it takes about 12 wingbeats to become airborne (figure 8).
The angular velocity of the body at take-off can be taken as an indication of the smoothness of the take-off [4]. For the fruit fly and butterfly, the maximum angular velocity is 2370 deg s\(^{-1}\) and 2000 deg s\(^{-1}\), respectively; but for the dronefly, the value is not more than 601 deg s\(^{-1}\). Another indication of the smoothness of the take-off is the acceleration of COM during take-off. The maximum vertical acceleration at take-off is about 6 \(g\) for the fruit fly [4] and about 10 \(g\) for the butterfly [6]. However, for the dronefly, this quantity is much smaller, less than 0.79 \(g\). For further comparison, time histories of body motion (velocity and acceleration of body COM and angular velocity and acceleration of body) of the fruit flies by Card & Dickinson [4] are plotted in figure 15. Comparing the fruit fly data in figure 15 with the dronefly data in figure 10 clearly shows that the acceleration of COM and angular velocity of body of the droneflies are much smaller than those of the fruit flies.

We thus see that compared with insects which take-off by jumping (locusts, milkweed bugs and fruit flies) or by ‘fling’ mechanism of wing-pair (butterfly), droneflies take-off relatively slowly but more smoothly.

Having compared the take-off behaviour and biomechanics among locust, milkweed bug, fruit fly, butterfly and dronefly, let us make some comments on the physiological or ecological aspects of the take-offs. As seen above, the locust, milkweed bug, fruit fly and butterfly perform fast take-off. Fast take-off involves large body angular velocity. If the angular velocity is not timely controlled, the insect might tumble. Fruit flies have halteres to get rotational sensory input in very short time and butterflies and moths might use antennae to quickly measure the angular velocity [24]. However, the milkweed bug and the locust do not have such rotational sensory system. Some sensory modalities capable of quickly sense rotations must be involved during take-off in these insects.

Similar to fruit flies, droneflies have halteres. But the droneflies choose not to use legs to jump but only use wing force to have slow and smooth take-off. This shows that the relative contributions of wings and legs to vertical force production may well vary phylogenetically among fly taxa. The slow take-off in droneflies might imply that they do not have...
Figure 13. Time histories of the horizontal components of the inertia force ($H_i$), aerodynamic force ($H_a$) and leg force ($H_{leg}$); the forces are non-dimensionalized by the weight of the insect, $mg; H_i^+ = H_i/mg, H_a^+ = H_a/mg$ and $H_{leg}^+ = H_{leg}/mg$. (a) DF1. (b) DF1a (the second take-off flight of dronefly DF1). (c) DF2. (d) DF2a (the second take-off flight of dronefly DF2). (e) DF3. $t = 0$ is the time when the COM of the insect body starts to raise (wing flapping begins before $t = 0$). The insect becomes airborne at ‘separating time’. (Online version in colour.)

Figure 14. Time histories of the (a) vertical ($V_a$) and (b) horizontal ($H_a$) components of the aerodynamic force of DF1, with and without the ground effect. The forces are non-dimensionalized by the weight of the insect, $mg: V_a^+ = V_a/mg$ and $H_a^+ = H_a/mg$. $t = 0$ is the time when the COM of the insect body starts to raise (wing flapping begins before $t = 0$). The insect becomes airborne at ‘separating time’. (Online version in colour.)
predators that attack them when perched. These need to be confirmed by future investigations.

4. Conclusion

In take-off, a dronefly increases its stroke amplitude gradually in the first 10–14 wingbeats and becomes airborne at about the 12th wingbeat. The aerodynamic force increases monotonously from zero to a value a little larger than its weight, and the leg force decreases monotonously from a value equal to the weight to zero, showing that the droneflies do not jump and only use the aerodynamic force of flapping wings to lift themselves into the air. Compared with take-offs in insects in previous studies, in which a very large force (5–10 times of the weight) generated either by jumping legs (locusts, milkweed bugs and fruit flies) or by ‘fling’ mechanism of wing-pair (butterflies) is used in a short time, the take-off in the droneflies is relatively slow but smoother.

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