Jumping from the surface of water by the long-legged fly *Hydrophorus* (Diptera, Dolichopodidae)

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**SUMMARY**
The fly *Hydrophorus alboflorens* (4 mm long, 4.7 mg mass) moves around upon and jumps from water without its tarsi penetrating the surface. All six tarsi have a surface area of 1.3 mm$^2$ in contact with the water, but they did not dimple its surface when standing. Jumping was propelled by depression of the trochanter of both hind and middle legs, which are 40% longer than the front legs and 170% longer than the body. As these four legs progressively propelled the insect to take-off, they each created dimples on the water surface that expanded in depth and area. No dimples were associated with the front legs, which were not moved in a consistent sequence. The wings opened while the legs were moving and then flapped at a frequency of 148 Hz. The body was accelerated in a mean time of 21 ms to a mean take-off velocity of 0.7 ms$^{-1}$. The best jumps reached velocities of 1.6 ms$^{-1}$, and required an energy output of 7 μJ and a power output of 0.6 mW, with the fly experiencing a force of 140 g. The required power output indicates that direct muscle contractions could propel the jump without the need for elaborate mechanisms for energy storage. Take-off trajectories were steep, with a mean of 87$^\circ$ to the horizontal. Take-off velocity fell if a propulsive tarsus penetrated the surface of the water. If more tarsi became submerged, take-off was not successful. A second strategy for take-off was powered only by the wings and was associated with slower (1 deg ms$^{-1}$ compared with 10 deg ms$^{-1}$ when jumping) and less extensive movements of the propulsive joints of the middle and hind legs. No dimples were then created on the surface of the water. When jumping was combined with wing flapping, the acceleration time to take-off was reduced by 84% and the take-off velocity was increased by 168%. Jumping can potentially therefore enhance survival when threatened by a potential predator.

**INTRODUCTION**
Living on or near water presents many hazards to an animal that breathes air. For a small insect the problem is accentuated by its size, which means that it risks being trapped by the surface tension of the water, or its fragile wings may become wet. Insects that have aquatic larval stages, such as mosquitoes or caddis flies, need to move from the surface of water when they emerge as adults. This risk of entrapment or drowning is apparently offset by the availability of food from others that have failed to avoid a similar fate. The fly *Hydrophorus* skates on the surface of water searching for a mate or preying upon other insects that have become trapped by the surface tension. While clearly at ease on the water surface, it may need to move to other sites or escape from predators within or above the water and thus launch into flight. Jumping enables it to launch more quickly into flight and avoid the risk of the flapping wings touching the water.

Solutions to the problem of moving around on water depend upon whether the properties of the surface tension are used, or whether the legs are propelled into the body of the water (Bush and Hu, 2006). Pond skaters make use of the surface tension to move around on the water surface and catch prey, propelled by rapid and synchronous rowing movements (Bowdan, 1977; Murphey, 1971) of their elongated and water-repellent middle legs (Gao and Jiang, 2004) that shed hemispherical vortices (Goodwyn et al., 2008; Hu et al., 2003). Some powerful propulsive strokes may lift the body clear of the water, thus resembling a jump, the distance of which may be prolonged by sliding on the low frictional surface of the water (Møller Andersen, 1982). By contrast, pygmy mole crickets jump from water by propelling their hind legs through the surface and pushing downwards a sufficient volume of water by the use of spring-loaded tibial paddles and spurs, which increase the surface area of the tibiae (Burrows and Sutton, 2012). Larger animals propel themselves by pushing a turbulent flow of fluid down with their feet, which must not become wet. This, for example, enables basilisk lizards (*Basiliscus*) to run for a few metres in a bipedal gait across the surface of water at a velocity of 1.5 ms$^{-1}$ (Rand and Marx, 1967) before sinking (Glasheen and McMahon, 1996; Hsieh, 2003; Hsieh and Lauder, 2004), and frogs to jump from the water (Nauwelaerts and Aerts, 2006; Nauwelaerts et al., 2004).

Few insects have transferred their jumping abilities on land to such compliant surfaces as water. On land, a few insects, such as bush crickets, extend their long jumping legs by direct muscular contractions (Burrows and Morris, 2003). The time taken to extend these long legs, and hence the period over which the body is accelerated, distributes the ground reaction forces that they exert over a longer time, but they are not reported to jump from the surface of water. Most hemipteran leafhoppers have hind legs that are as much as 230% longer than the front legs, but a closely related group,
the Ulopinae, has hind legs that are no more than 10% longer than the other legs. Both groups have similar take-off velocities, but there are marked differences in their acceleration times and hence ground reaction forces (Burrows and Sutton, 2008). The advantage of their long legs may again lie in distributing ground reaction forces over a longer time, thus reducing energy losses when taking off from compliant surfaces such as thin and pliable leaves, or even water. Slow movements of long legs will thus produce lower ground reaction forces.

By contrast, most insects, including grasshoppers (Bennet-Clark, 1975), fleas (Bennet-Clark and Lucey, 1967; Sutton and Burrows, 2011) and many families of bugs within the Hemiptera [e.g. froghoppers (Burrows, 2003; Burrows, 2006), leafhoppers (Burrows, 2007) and planthoppers (Burrows, 2009a)] use catapult mechanisms for jumping in which power is applied in a very short time. Again, none are reported to be able to jump from water, but different species can jump from surfaces of different compliances by having propulsive legs of different lengths.

This paper reports on an analysis of a fly that successfully jumps from the surface of water. *Hydrophorus* has much longer legs, and feet with a large surface area in contact with the water, in contrast to flies such as *Drosophila*, which jump from land (Card and Dickinson, 2008; Trimarchi and Schneiderman, 1995; Zumstein et al., 2004). The middle and hind legs act together to provide the propulsive force for jumping and their contribution can be gauged by the dimpling of the water surface that they each cause. The tarsi do not penetrate the surface. Jumping increases the velocity of take-off and hence a launch into flight by 168%, and decreases the time to take-off by 84% compared with an alternative strategy of flying accompanied by leg movements that do not cause dimples in the water surface.

**MATERIALS AND METHODS**

*Hydrophorus alboflorens* (Walker 1849) were collected from lagoons, ponds and puddles in forest tracks around Halifax, Nova Scotia, Canada, during September to November 2010. They belong to the order Diptera, sub-order Brachycera, super-family Empidioidea, family Dolichopodidae and sub-family Hydrophorinae.

Sequential images of jumps were captured at rates of 5000 s⁻¹ and an exposure time of 0.1 or 0.2 ms, with a single Photon Fastcam 512PCI camera (Photon Europe, High Wycombe, Bucks, UK), fitted with a 100 mm micro Tokina lens. Images were fed directly to a portable computer for later analysis. All jumps occurred spontaneously from the water contained within a glass chamber measuring 80 mm wide, 80 mm high and 25 mm deep. Some spontaneous jumps were also from the walls of the chamber. The camera pointed either at an angle above the surface of the water or directly at the meniscus of the water in the middle of the front face of the chamber. Measurements of changes in joint angles and distances moved were made from jumps that were, as close as possible, parallel to the image plane of the camera. Jumps that deviated from this plane by ±30° were calculated to result in a maximum error of 10% in the measurements of joint or body angles. Peak velocity was calculated as the distance moved by a point on the thorax just dorsal to the middle legs and measured from such sequences. A rolling three-point average of successive images was taken during the final 3 ms before take-off. Other jumps in which the insect was viewed from behind or in front were also captured. A total of 60 jumps by six adult *H. alboflorens* were captured, with a minimum of three jumps by each fly. Two jumping sequences are included as supplementary material Movies 1, 2. Selected image files were analysed with Motionscope camera software (Redlake Imaging, Tucson, AZ, USA) or with Canvas 12 (ACD Systems of America, Miami, FL, USA). The time at which the hind legs lost contact with the water surface and became airborne was designated as time \( t = 0 \) ms in Figs 2, 3, 4 and 6, so that different jumps could be aligned and compared. The time at which the middle or hind legs started to move and propel the jump was also labelled and the time between these two events defined the period over which the body was accelerated in a jump. A one-frame error in estimating both the first movement of the hind legs and the take-off time would result in a 10% error in measuring acceleration time. Measurements are given as means ± s.e.m. Temperatures within the experimental chamber ranged from 22 to 24°C.

Photographs of live flies were taken with a Nikon D90 camera fitted with a 100 mm Nikon macro lens. The anatomy of the legs was examined in intact flies, and in those fixed and stored in 70% alcohol or 50% glycerol. Dried specimens were mounted on specimen holders, sputter coated with gold and then examined in an XL-30 FEG scanning electron microscope (Philips, Eindhoven, The Netherlands). Lengths of the legs of fixed specimens were measured to an accuracy of 0.1 mm on images captured with a digital camera attached to a Leica MZ16 microscope (Wetzlar, Germany) and projected onto a large monitor. Body masses were determined to an accuracy of 0.1 mg with a Mettler Toledo AB104 balance (Beaumont Leys, Leicester, UK).

**RESULTS**

**Behaviour**

*Hydophorus alboflorens* (Fig. 1) was observed in its natural environment flying low over calm lagoons, ponds and puddles of
fresh water, occasionally alighting briefly on the surface of the water, and then standing or moving about on the water for prolonged periods. When on the surface of the water, the body and the wings did not become wet. In response to a shadow or a vibrational stimulus to the water surface they would jump and launch into flight with a wingbeat frequency of 148±1 Hz (grand mean ± s.e.m. of six *H. alboflorens*). Many jumps, however, appeared to be spontaneous or at least not in response to any discernible stimulus. The same flies would also alight upon, and take-off from, the surrounding vegetation.

**Body form**

Adult *H. alboflorens* had a body length of 4.4±0.2 mm and a mass of 4.7±0.6 mg (*N*=8). There were no apparent size classes within the flies studied and thus they were not divided into males and females. The body was narrow with a maximum width of 1 mm and the wings projected posteriorly over the body and beyond the tip of the abdomen when folded (Fig. 1A,B). All the legs were longer than the body, thus fulfilling the common name of this family of flies – long-legged flies; the front legs were 5.3±0.1 mm long, the middle legs 7.1±0.1 and the hind legs 7.3±0.1, so that the ratio of leg lengths was 1:1.4:1.4 (front:middle:hind). The front legs were 122% longer than the body, the middle legs 165% longer, and the hind legs 170% longer. Expressing the length of the hind and middle leg against the cube root of the body mass gave a ratio of 4.4.

When standing on water, reflections indicated that the entire length of all six tarsi were in contact with, but did not penetrate, the surface (Fig. 1B). The tarsus of the front leg was 1.6 mm long, the middle 2 mm and the hind 2.1 mm long. This means that for each leg the tarsus was long relative to both the femur and tibia; the front leg tarsus was 127% longer than front tibia and 114% longer than the front femur, for the middle legs the values were 93 and 97% and for the hind legs 91 and 89%. All tarsi had a width of 120–125 μm, as measured from images captured in the scanning electron microscope, so that all six tarsi provide a contact area of 1.3 mm^2 (0.2 mm^2 for a front, 0.21 mm^2 for a middle and 0.25 mm^2 for a hind tarsus) when on the surface of the water (Fig. 1B).

**Kinematics of jumping**

High-speed images of jumps from the surface of the water were captured from different angles by a single camera (Figs 2–4) so that the orientation and movements of the legs could be interpreted in all three dimensions. The majority of the jumps were viewed from the side (Fig. 2, supplementary material Movie 1), augmented by views from behind (Fig. 3) and in front (Fig. 4). Some jumps were performed from the front glass wall of the chamber, allowing the leg movements to be seen from underneath. For most jumps, the camera pointed at an angle down onto the surface of the water to record any ripples created by forces applied by individual legs. To determine whether any leg penetrated the surface of the water, the camera was also pointed in the plane of the water surface. The following description combines information from all views and applies to all jumps that occurred spontaneously and after variable periods of standing on the water.

When standing on the water in advance of a jump, all six tarsi were in full contact with the surface of the water but none caused marked dimpling. Jumping was propelled by the depression of the trochantera of both middle and both hind legs that usually preceded opening and then flapping movements of the wings (Figs 2–4). The first movements of the middle and hind legs were synchronised to within 1 ms of each other. The front legs, by contrast, showed no consistent pattern of movement from jump to jump that indicated they were contributing to propulsion. Typically, they were lifted from the surface of the water before take-off occurred and while the middle and hind legs depressed at their coxo-trochanteral joints. At no stage during a jump did the front tarsi create dimples in the
water. By contrast, the movements of the middle and hind legs created dimples around their tarsi that increased in depth and diameter the further the body was raised from the water (Figs 2–4). These dimples indicate that these four legs – two middle and two hind – were applying force to the water surface.

When jumping was viewed in the same plane as the surface of the water, the following features of the movements of the tarsi became apparent (Fig. 5). First, the tarsi of the hind and middle legs did not penetrate the surface of the water when creating large dimples (Fig. 5A–C). A tarsus could be seen below the meniscus of the chamber but still above the indented surface of the water. Air could sometimes be seen to be present surrounding the tarsus (Fig. 5B). In other sequences the indentation of the water below the meniscus could be seen to change in depth and in shape as force was applied.

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**Fig. 3.** *Hydrophorus alboflorens* jumping from the surface of the water viewed from behind. Images were captured at 5000 s⁻¹. When standing the six legs made only small indentations in the surface. As soon as the middle and hind legs started to depress and extend they created large dimples that expanded progressively.

**Fig. 4.** *Hydrophorus alboflorens* jumping from the surface of the water viewed from the front. Images were captured at 5000 s⁻¹. The front legs lost contact with the water surface earlier than the middle and hind legs and, unlike the middle and hind legs, did not cause indentations in the surface of the water.
Fly jumping from water

and then reduced as the leg was progressively lifted from the water (Fig. 5C). These observations indicate that the tarsi normally remained above the surface of the water.

In normal jumps, in which no legs penetrated the surface of the water, the time taken to accelerate the body to take-off was 21.1±0.2 ms (grand mean for six flies with a minimum of three jumps by each; Table 1). The mean take-off velocity was 0.7±0.06 m s⁻¹, with the best performance by an individual fly achieving 1.6 m s⁻¹.

In the best jumps, the applied accelerations were 140 m s⁻² so that the forces experienced were approximately 14g. The energy required to achieve take-off ranged from 1.2 μJ in average jumps to 7.2 μJ in the best jumps. The power output ranged from 0.1 to 0.6 mW, and the force exerted in the best jumps was 0.8 mN. The mean take-off angle was a steep 87±5 deg relative to the horizontal. The wings were usually being depressed at take-off, but the relationship between the leg and wing movements was variable, and take-off could occur at the start or end of depression within either the first or second wingbeat cycle.

In some jumps, one of the middle or hind legs did penetrate the surface of the water and was then moved in the water (Fig. 5D). The fly nevertheless still managed to take-off, but at a lower velocity. For example, in a jump in which at least one leg penetrated the

Table 1. Performance of Hydrophorus alboflorens when jumping from the surface of water

<table>
<thead>
<tr>
<th>Formula</th>
<th>Body mass (m)</th>
<th>Body length</th>
<th>Time to take-off (t)</th>
<th>Take-off velocity (v)</th>
<th>Take-off angle (f)</th>
<th>Acceleration (a)</th>
<th>g force (g)</th>
<th>Energy (E)</th>
<th>Power (p)</th>
<th>Force (F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Units</td>
<td>mg (10⁻⁶ kg)</td>
<td>mm</td>
<td>ms (10⁻⁴ s)</td>
<td>m s⁻²</td>
<td>deg</td>
<td>m s⁻²</td>
<td>g</td>
<td>μJ (10⁻⁶ J)</td>
<td>mW (10⁻⁴ W)</td>
<td>mN (10⁻⁵ N)</td>
</tr>
<tr>
<td>Jumping and flying</td>
<td>4.7±0.6</td>
<td>4.4±0.2</td>
<td>21.1±1.4</td>
<td>0.70±0.06</td>
<td>87±5</td>
<td>33.3</td>
<td>3.4</td>
<td>1.2</td>
<td>0.1</td>
<td>0.2</td>
</tr>
<tr>
<td>Best</td>
<td>5.3</td>
<td>4</td>
<td>11.6</td>
<td>1.64</td>
<td>80</td>
<td>141.4</td>
<td>14.4</td>
<td>7.2</td>
<td>0.6</td>
<td>0.8</td>
</tr>
<tr>
<td>Flying only</td>
<td>4.7±0.6</td>
<td>4.4±0.2</td>
<td>32.4</td>
<td>0.38</td>
<td>68</td>
<td>11.7</td>
<td>1.2</td>
<td>0.4</td>
<td>0.01</td>
<td>0.1</td>
</tr>
<tr>
<td>Best</td>
<td>5.4</td>
<td>4</td>
<td>25.2</td>
<td>0.43</td>
<td>43</td>
<td>17.1</td>
<td>1.7</td>
<td>0.5</td>
<td>0.02</td>
<td>0.1</td>
</tr>
</tbody>
</table>

The first row gives the mean of means take-off performance for 6 flies when jumping and flying, and the second the best performance of an individual. The third row gives the mean performance for 6 take-offs by the same 6 flies when flying alone was used and there was no disturbance of the water surface; the last line gives the best performance by an individual.
surface (Fig. 5D), the take-off velocity of 0.43 m s\(^{-1}\) was 63% lower than the average.

**Take-off into flight without jumping**

In eight of the 60 sequences of taking off by *H. alboflorens*, the middle and hind legs did not cause any indentations in the surface of the water, indicating that they were not applying much force (Fig. 6, supplementary material Movie2). The wings were, however, still flapped at the same frequency (Figs 2–4). With this strategy, it took longer to accelerate the body to take-off (35±4 ms, mean of six take-offs), compared with a mean of 19±2 ms for a further six take-offs accompanied by jumping by the same individual *H. alboflorens*. The take-off velocity was also lower (0.38±0.16 m s\(^{-1}\)) compared with 1.02±0.15 m s\(^{-1}\), for those assisted by jumping. These values are statistically significantly different (*t*-test with equal variance not assumed: acceleration time \(t_{6.292}=3.66, P=0.01\); take-off velocity \(t_{5.125}=4.29, P=0.007\)). The longer acceleration time also meant that the wings could complete more cycles of flapping movements before take-off. The differences between the movements of the middle and hind legs in these two strategies became clearer when angular changes were plotted for two joints of a hind and a middle leg (Fig. 7). When jumping, the angle through which the femur was moved relative to the body, and by the tibia relative to the femur, in both the middle and hind legs ranged from 60 to 100 deg. By contrast, when flying alone appeared to power take-off, the joints moved through less than 50 deg. The rate of angular changes in the joints was also much lower. For example, when jumping the rate of angular movement by the right and left middle femora about the body was approximately 10 deg s\(^{-1}\), but fell to only 1 deg s\(^{-1}\) when flying alone was used.

**Landing on the surface of water**

When alighting on water, *H. alboflorens* also had to ensure that its body and especially its wings did not become wet, to avoid the risk of becoming trapped by the surface tension. A small number of landings were captured when they fortuitously happened in the focal plane of the camera (Fig. 8). The fly approached the water with all six legs outstretched, the front legs pointing anteriorly and the middle and hind legs sideways. In the example shown, the body was tilted sideways in such a way that the distal tips of the tarsi of the left middle and hind legs were the first to contact the water (Fig. 8). The wings were in the elevated phase of the flight sequence. The left middle and hind tarsi, together with the wing movements, were able to support the mass of the body and did not penetrate the surface. The body then tilted to the right so that the entire lengths of the middle and hind tarsi contacted the surface of water and the tip of the abdomen indented the surface, but did not penetrate it. The right middle and hind tarsi next contacted the water and finally the front tarsi touched down. Throughout this sequence the hind wings were held above the surface and at no time did any part of the fly penetrate the surface. The result was that only the under-surfaces of the abdomen and the tarsi contacted the water surface. The wake caused by the impact of the fly then spread out, with the fly coming to rest with all tarsi in contact with the water but not associated with any dimpling of the surface.

**DISCUSSION**

This study has demonstrated that to jump successfully and rapidly from the surface of water *H. alboflorens* uses three morphological specialisations and two behavioural strategies. The body structure spreads the propulsive forces over a large area of contact between the legs and the water surface in both space and time. In addition, the two behavioural strategies produce take-offs that differ in the time it takes to become airborne and in the take-off velocity. Jumps were accompanied by, or followed by, flapping movements of the wings and thus represent a mechanism for launching into flight. The key to successful jumping was that the fly made use of the surface tension of the water. If the tarsi of the propulsive legs penetrated the surface, take-off velocity was either reduced or failed completely, with the attendant risk of the body either becoming wet or entrapped by the surface tension.

**Structural specialisations**

The three key specialisations used in jumping from water are the way that the propulsive (ground reaction) forces are applied. First, the simultaneous contribution of the middle and hind legs distributes...
these forces between four points of tarsal contact with the water. Second, the long middle and hind legs (165–170% longer than the body) distribute the forces over a mean acceleration time of 21 ms. This is because it takes longer to extend longer legs, and therefore the forces exerted on the water at any one time will be lower than if the legs were shorter. Third, each tarsus is long and covered in numerous fine hairs so that the surface area of contact of the four propulsive tarsi is 0.92 mm\(^{-2}\). The front tarsi are longer than the front femur or tibia and the propulsive middle and hind tarsi are almost as long as their respective femora and tibiae. All of these factors combine to ensure that the forces applied by the propulsive legs are distributed widely. The importance of not penetrating the surface tension is emphasised by the consequences that result when, on rare occasions, a leg is pushed into the water. The take-off velocity is then reduced by half even if the other legs remain on the surface. If more than one tarsus penetrates the surface the remaining ground reaction forces may not be able to raise the body sufficiently from the water to allow the wings to move without contacting the water and becoming entrapped. The same specialisations also allow the fly to land on the surface of the water without becoming wet.

**Behavioural strategies**

*Hydrophorus alboflorens* used two distinct strategies to take-off from the surface of water and launch into flight: first, propulsion by the combined actions of the middle and hind legs in jumping and the wings in flapping; and second, by the flapping movements of the wings at the same frequency, but with a lesser contribution from the middle and hind legs – their rate of angular movement was tenfold less, and the angles through which particular joints moved were halved. The combination of these two resulted in leg movements that took longer to accelerate the fly to take-off. They also resulted in a reduction of the ground reaction forces exerted, as deduced from the absence of dimpling of the water surface normally associated with the tarsi of each of these legs when jumping. The two strategies were not used by an individual fly in any particular sequence, but in the experimental chamber used to capture high-speed images, combined jumping and flying was the predominant mechanism in all flies analysed. Because all the jumps were spontaneous, it is not clear whether specific stimuli elicit, as they do in *Drosophila* (Card and Dickinson, 2008), different jumping performances.

The contribution of jumping was to reduce the time taken to become airborne (the acceleration time) by 84% and to increase the take-off velocity by 168%. Both effects should markedly increase survival chances in escaping from a potential predator approaching from below the water surface, or from above. There is a balance, however, between speed of escape and the risk that too much force applied too rapidly will result in the tarsi penetrating the water; this would reduce take-off velocity, or lead to a possible failure of take-off altogether. Both strategies, coupled with the length of the middle and hind legs, ensure that the body is raised high enough above the
Jumping performance

A jump by *H. alboflorens* required the coordinated action of four legs, which all started to move within 1 ms of each other, as measured from the high-speed images, and their movements paralleled each other during the acceleration phase of a jump. This level of synchrony between the legs is similar to that seen in grasshoppers and locusts, where the legs, like those of the fly, move in separate planes parallel to the sides of the body (Sutton and Burrows, 2008). In insects where the propulsive hind legs are arranged beneath the body and move in the same plane as each other parallel to the under surface of the body, much closer synchronisation is necessary to control jump trajectory in the azimuth plane (Sutton and Burrows, 2010).

Can direct contractions of the trochanteral depressor muscles generate sufficient force during the acceleration period to lift the fly from the surface of the water, or must some form of energy storage and a power amplification mechanism be used? In most jumping insects, such as grasshoppers (Bennet-Clark, 1975) and hemipteran hoppers (Burrows, 2006), a jump is powered only by the two hind legs with the mass of their jumping muscles representing approximately 10–11% of total body mass. If the jumping muscles of *H. alboflorens* follow the same proportional relationship, a power output of some 120 W kg⁻¹ of muscle, as calculated from the kinematics, would be needed to generate one of the best jumps. Because two pairs of legs propel a jump, the proportion of jumping muscle mass may be higher, further lowering the power output required. The maximum active contractile limits of normal muscle range from 250 and 500 W kg⁻¹ (Askew and Marsh, 2002; Ellington, 1985; Josephson, 1993; Weis-Fogh and Alexander, 1977), so that the calculated values for *H. alboflorens* are therefore well within this range. Direct contractions of the appropriate trochanteral muscles in the hind and middle leg muscles should be capable of propelling a jump. It follows, therefore, that these flies do not need to store energy and then release it suddenly in a catapult-like mechanism, and elaborate energy storage mechanisms are not required.

The overall jumping performance nevertheless matches those of some other insects that jump from land by the direct contractions of muscles. For example, *Drosophila* reaches an initial velocity of 0.5 m s⁻¹ in an acceleration time of 5 ms when jumping from land (Card and Dickinson, 2008). Similarly, snow fleas (Mecoptera, Boreidae) use direct contractions of middle and hind legs muscles to propel themselves to take-off velocities of 1.0 m s⁻¹ in approximately 6 ms, again when jumping from land (Burrows, 2011). With this method of jumping, performance can be improved by increasing the length of the hind legs and thus their leverage. This option is exploited by bush crickets that can achieve take-off velocities of 2 m s⁻¹ but at the expense of much longer acceleration times (Burrows and Morris, 2003).

The jumping performance of *H. alboflorens* approaches that of jumping insects that do use a catapult mechanism, even though *H. alboflorens* is jumping from a compliant surface. Two hemipteran bugs, *Hackeriella* (Coleorrhyncha: Peloridiidae) (Burrows et al., 2007) and *Saldula* (Heteroptera: Saldidae) (Burrows, 2009b), reach take-off velocities of 1.5 and 1.8 m s⁻¹ but accelerate in only 2–4 ms so that the energy requirements are much higher. The champion jumping insects in terms of take-off velocity are some froghoppers (Burrows, 2003; Burrows, 2006) and some planthoppers (Burrows, 2009a), which achieve their prowess by transferring energy stored in a catapult in less than 1 ms. A consequence of this is that the ground reaction forces are unsuitably high for jumping from a compliant surface such as water; the propulsive legs would penetrate the surface. Pygmy mole crickets that also use a catapult deliberately penetrate the surface of the water with their propulsive tibiae, but have spring-loaded tibial paddles that flare out to increase the tibial surface area and enable a sufficient volume of water to be pushed downwards (Burrows and Sutton, 2012).

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COMPETING INTERESTS

No competing interests declared.
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REFERENCES


Movie 1. *Hydrophorus alboflorens* jumping and flying from the water. Rear view of a take-off in which the middle and hind legs cause four indentations in the surface of the water. Images were captured at a rate of 5000 s\(^{-1}\) and with an exposure time of 0.2 ms and are replayed at a rate of 30 frames s\(^{-1}\).

Movie 2. Flying from the surface of the water. Rear view of take-off by the same fly, in which the middle and hind legs did not cause any indentations in the surface of the water. Images were captured at a rate of 5000 s\(^{-1}\) and with an exposure time of 0.2 ms and are replayed at a rate of 30 frames s\(^{-1}\).