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RESEARCH ARTICLE

Jumping mechanisms in adult caddis flies (Insecta, Trichoptera)

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ABSTRACT

To understand the jumping mechanisms and strategies of adult caddis flies, leg morphology and movements were analysed in three species with mean masses of 3.9 to 38 mg. Two distinct jumping strategies were found. First (67% of 90 jumps), take-off was propelled solely by the middle and hind legs while the wings remained closed. Second (33% of jumps), the same leg movements were combined with wing movements before take-off. The hind legs were 70% and the middle legs were 50% longer than the front legs and represented 105% and 88%, respectively, of body length. Both hind and middle trochantera were depressed together, approximately 15 ms before take-off. The front legs apparently did not contribute to thrust in either strategy and were the first to be lifted from the ground. The hind legs were the next to lose contact, so that the middle legs alone provided the final thrust before take-off. Jumping performance did not differ significantly in the two jumping strategies or between species, in acceleration times (range of means for the three species 14.5–15.4 ms), take-off velocities (range 0.7–1 m s^{-1}) and trajectory angles. A significant difference in jumps propelled only by the legs was the lower angle (9.3± 1.9 deg) of the body relative to the horizontal at take-off compared with jumps involving wing movements (35.3±2.5 deg). Calculations from the kinematics indicated that jumps were produced by direct muscle contractions and did not require power amplification or energy storage.

KEY WORDS: Kinematics, High speed imaging, Locomotion, Flying, Escape movements

INTRODUCTION

The need for a rapid means of escaping from predators appears to have been a strong force driving the evolution of jumping in many orders of insects. The diversity of habitats that insects have come to occupy, however, has meant that other pressures on locomotion also exist. When flight is the dominant form of locomotion, the need to launch effectively and rapidly into flight becomes a key feature of survival. Many insects thus use legs and wings in various sequences and combinations to escape and to launch into flight with advantages and disadvantages to any particular strategy.

A common technique for jumping is to use a single pair of propulsive legs alone and to hold the wings firmly folded so that take-off velocity is not slowed by the drag from the large surface area of the moving wings. This method has elevated some froghoppers and planthoppers to the rank of the fastest jumpers amongst all insects (Burrows, 2006, 2009). Other insects such as some flies (Card and Dickinson, 2008) may use only their middle legs while still others such as snow fleas (Burrows, 2011) and moths (Burrows and Dorosenko, 2015) may use the middle and hind legs together. Combining such propulsive leg movements with movements of the wings may be used for two reasons. First, the thrust from wing movements can reduce the ground reaction forces through the legs, thus enabling take-off from more pliant surfaces. For example, when jumping from the surface of water, the fly *Hydrophorus alboflorens* can use just flapping movements of its wings, but when the legs are also used, take-off time is reduced by 84% and take-off velocity is increased by 168% (Burrows, 2013). The downside to using the legs is that if too much force is applied, the tarsi will penetrate the water surface with the danger that the body will be wetted and drowning becomes a reality. Second, in insects such as lacewings (Burrows and Dorosenko, 2014) the propulsive jumping movements of the legs add additional thrust before the wings can act fully and they also raise the body from the ground, allowing an earlier full depression of the wings without risking damage that would result from them striking the ground. These considerations become especially germane in heavier insects and in those with large wings such as butterflies and moths.

Analyses of the complex movements of the wings of butterflies at take-off into flight (Sunada et al., 1993) indicate the forces produced by the wings alone are insufficient to achieve take-off (Bimbard et al., 2013). Most moths are also adept at launching into flight, and some wingless species are able to propel themselves forward for distances of about 10 cm or 10 body lengths (Medeiros and Dudley, 2012). A kinematic analysis of the leg movements of winged moths shows that the legs alone can propel a jump (Burrows and Dorosenko, 2015). Wing movements can also be used by moths in some jumps so that there are three distinct strategies for becoming airborne. First, rapid movements of the middle and hind legs moving together provide propulsion while the wings remain closed. In this strategy, the wings could remain closed until landing. Second, the middle and hind legs again provide propulsion but the wings now open and begin to beat after take-off so that the jump leads directly to flight. Third, wing and leg movements both begin before take-off and lead to an even earlier transition to powered flight. Individual moths can use any of the three strategies, but the first is used more frequently by smaller moths, whilst larger moths more often supplement leg movements by opening and moving the wings before take-off.

Close relatives of the Lepidoptera are the Trichoptera, which includes caddis flies (they all belong to the superorder Amphiesmenoptera). This relationship is supported by evidence from molecular (Wheeler et al., 2001; Whiting, 2002), morphological (Wheeler et al., 2001; Whiting, 2002) and paleontological (Grimaldi and Engel, 2005) studies, even though Trichoptera have aquatic larvae and as adults generally have hairy rather than scaly bodies and wings. Most experimental work on the locomotion and behaviour of this group has focused on the larvae with few analyses of the adults. There are some details of adult anatomy (Korboot, 1964), of their feeding (Crichton, 1957) and of their mating behaviour in swarms (Petersson, 1995), but there appear to be no reports of jumping. This paper establishes that jumping is part of the locomotory repertoire of adult caddis flies and then analyses the propulsive mechanisms and the strategies that they use to launch themselves into the air.

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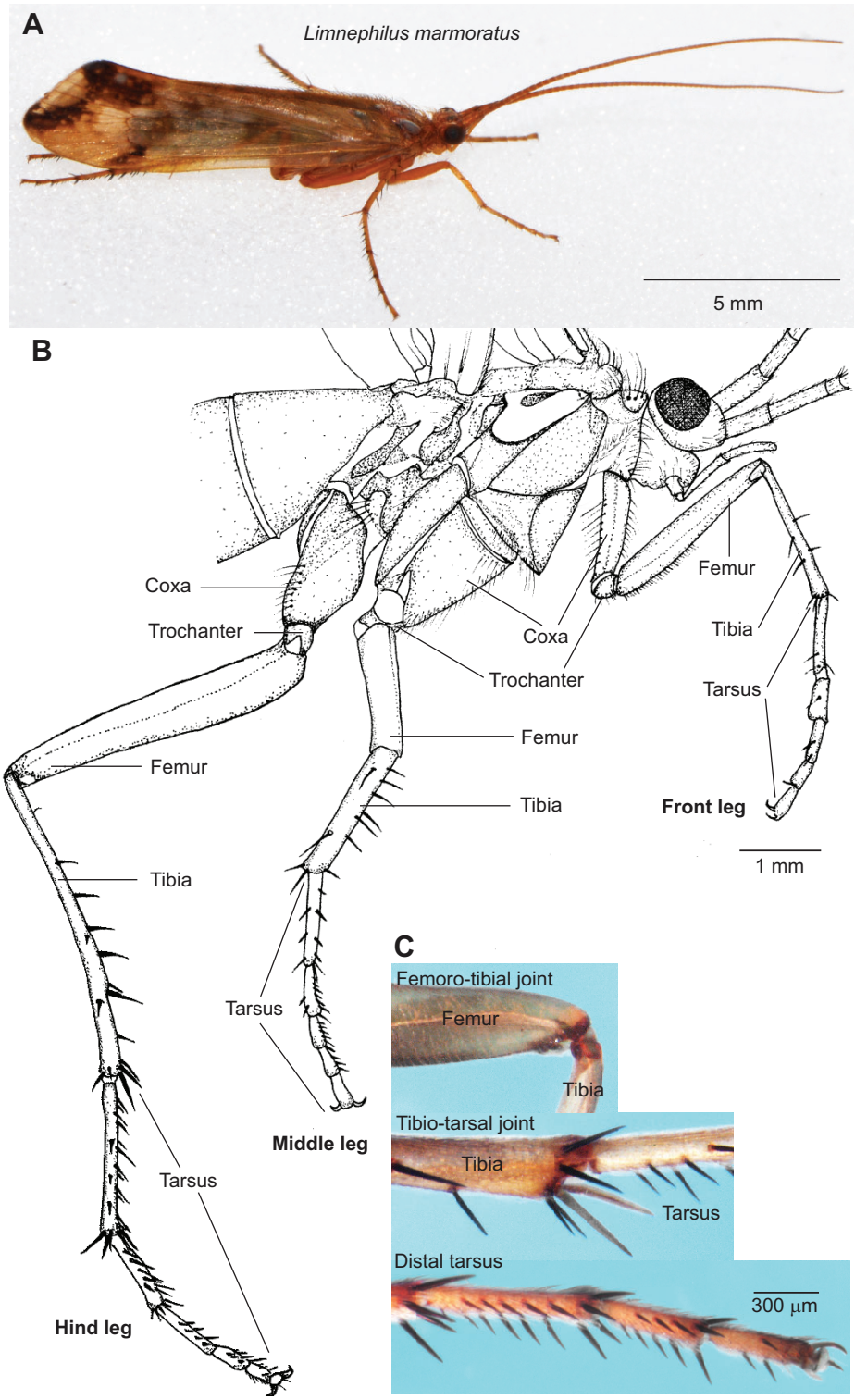

Fig. 1. Body form of the caddis fly *Limnephilus marmoratus* as related to jumping. (A) Photograph of an adult female viewed from the side. (B) Drawing of a side view of an adult male to show the structure of the thorax and the legs. The middle and hind legs are close together and the hind coxa subtends a different angle to the thorax as compared with the middle coxa. (C) Photographs of the femoro-tibial and tibio-tarsal joints of a hind leg, and of the distal three segments of a tarsus.

RESULTS

Shape of body and legs

When folded, the wings of adult caddis flies were triangular and projected a few millimetres beyond the posterior tip of the abdomen where they touched the ground when the caddis fly was standing (Fig. 1A). The antennae were 25% longer than the length of the body (measured from the head to the tip of the abdomen). The largest of the three species analysed, *Limnephilus marmoratus*, had a body length of 11.4±1.1 mm and a mass of 38.1±2.4 mg (means± s.e.m., N=19) (Table 1); *Molanna angustata* was 9.3±0.7 mm long

Table 1. Jumping performance of caddis flies

	Body mass (*m*)	Body length	Acc. time (*t*)	Take-off velocity (*v*)	Acc.	***g*** force	Energy (*E*)	Power (*p*)	Force (**F**)	Power/muscle mass
Formula					$f=v/t$	$g=f/9.81$	$E=0.5mv^2$	$p=E/t$	$F=mf$	$p/0.1m$
Units	mg	mm	ms	m s^{-1}	m s^{-2}	***g***	μJ	mW	mN	W kg^{-1}
L. marmoratus										
Mean (*N*=8)	38.1±2.4 (*N*=19)	11.4±0.3 (*N*=19)	15.4±0.8	0.9±0.04	57	6	16.4	1	12.3	256
Best	50		17	1.1	64	6	29.2	1.7	3.2	343
M. angustata										
Mean (*N*=2)	11.3±1.1 (*N*=7)	9.3±0.7 (*N*=7)	15	1	64	7	5.2	0.4	0.7	307
Best	8		17	1.1	62	6	6.6	0.4	0.7	343
M. azurea										
Mean (*N*=2)	3.9±0.2 (*N*=24)	5.0±0.1 (*N*=24)	14.5	0.7	51	5	1.1	0.1	0.2	186
Best	6		16	0.9	53	5	1.4	0.1	0.2	226

The jumping performance of three species of caddis flies analysed: *Limnephilus marmoratus*, *Molanna angustata* and *Mystacides azurea*. Data in columns 2–5 are the mean of means for the body size and jumping performance of (*N*) individuals of each species (±s.e.m.); the best performance (defined by the fastest take-off velocity) of a particular individual is also given. The calculated values in columns 6–11 on the right are derived from these measured data. Acc., acceleration.

and had a mass of 11.3±1.1 mg (*N*=7), while the smallest, *Mystacides azurea* was 5.0±0.1 mm long and had a mass of 3.9±0.2 mg (*N*=24). The legs were long and thin in all three species; in *L. marmoratus*, the front legs were 7.0±0.3 mm long, the middle legs were 10.2±0.5 mm and the hind legs were 12.2±0.6 mm (*N*=7 caddis flies; Table 2). This gave a ratio of leg lengths, relative to the front legs, of 1:1.5:1.7 (front:middle:hind). The front legs were 60% of body length, the middle legs were 88% and the hind legs were 105%. The longest segments in all three pairs of legs were the tarsi; in the front and middle legs they were 50% longer than their respective tibiae and in the hind legs they were 25% longer. The long length of a hind leg was attributable to its elongated tibia and tarsus, which were 128% and 88% longer, respectively, than those segments of a front leg and 52% and 21% longer, respectively, than those of a middle leg (Table 2, Fig. 1B). The length of the hind legs of *L. marmoratus* when expressed relative to the cube root of body mass gave a ratio of 3.6 and the middle legs gave a ratio of 3.0.

The coxae of both middle and hind legs were much enlarged compared with those of the front legs and were oriented in such a way that the legs pointed in different directions (Fig. 2A): the middle legs pointed laterally, the hind legs posteriorly and the front legs forwards. The coxae of the middle and hind legs were also closely opposed at the ventral midline (Fig. 2B). The short middle and hind trochantera were able to rotate through approximately 100 deg about their respective coxae so that when fully levated, and because the joint of the trochantera with the femora allowed less rotation, they swung the femora forwards to lie closely against the lateral surface of the coxae. The hind tibiae were bowed with a radius of curvature of 11 mm, whereas the tibiae of the front and middle legs were straight (Fig. 1B). The tibiae and tarsi of all legs had a series of spines and spurs that were more numerous at the joint of a tibia with a tarsus and at the joints of tarsal segments (Fig. 1C) that would all contact the ground when standing and preparing to jump.

Jumping kinematics

Two distinct strategies for jumping were used by all three species of caddis fly in the 90 jumps that were recorded and analysed. In the first strategy, 60 jumps (67%) were propelled by rapid movements of the middle and hind pairs of legs alone whilst the wings remained closed (Figs 3–5 and Fig. 6A; supplementary material Movies 1 and 2). In the second strategy used in 30 jumps (33% of the total), the middle and hind legs repeated their same sequence and pattern of movements, but the wings were now opened and were being depressed before take-off was achieved (Fig. 6B, Figs 7, 8; supplementary material Movie 3). Wing movements (strategy 2) accompanied 42% of the spontaneous jumps but only 8% of jumps elicited by a mechanical stimulus.

The following description of the movements of the legs is based on jumps in the first strategy for jumping but applies equally to the second strategy.

First strategy for jumping

The first propulsive movements of the middle and hind legs occurred within 1 ms of each other as determined by the resolution of 1 ms given by a frame rate of 1000 frames s^{-1} (Figs 3–5). As viewed from the side, the leg movements were apparent as backward movements of the femora caused by depression of the trochantera about the coxae. The progressive depression of the trochantera was accompanied by extension of the tibiae about the femora so that the whole leg was straightened. The hind legs reached their most depressed and extended positions and lost contact with the ground just before take-off in *L. marmoratus* (Fig. 3; supplementary material Movie 1), *M. angustata* (Fig. 4; supplementary material Movie 2) and *M. azurea* (Fig. 5). In 95% of all jumps, the hind legs lost contact with the ground before the middle legs. In the remaining 5% of jumps, the hind and middle legs left the ground at the same time. The mean difference in time between the hind and middle legs leaving the ground was 3.48±0.36 ms for *L. marmoratus*, 3.04±0.29 ms for *M. angustata* and 3.14±0.34 ms for *M. azurea*. These

Table 2. Leg lengths of *Limnephilus marmoratus*

	Femur (mm)	Tibia (mm)	Tarsus (mm)	Whole leg (mm)	Ratio of leg lengths	% Body length
Front leg	2.2±0.1	1.8±0.1	2.7±0.1	7.0±0.3	1	60
Middle leg	2.9±0.2	2.7±0.2	4.2±0.2	10.2±0.5	1.5	88
Hind leg	2.5±0.2	4.1±0.3	5.1±0.2	12.2±0.6	1.7	105

Data are the means±s.e.m. for seven caddis flies of this species.

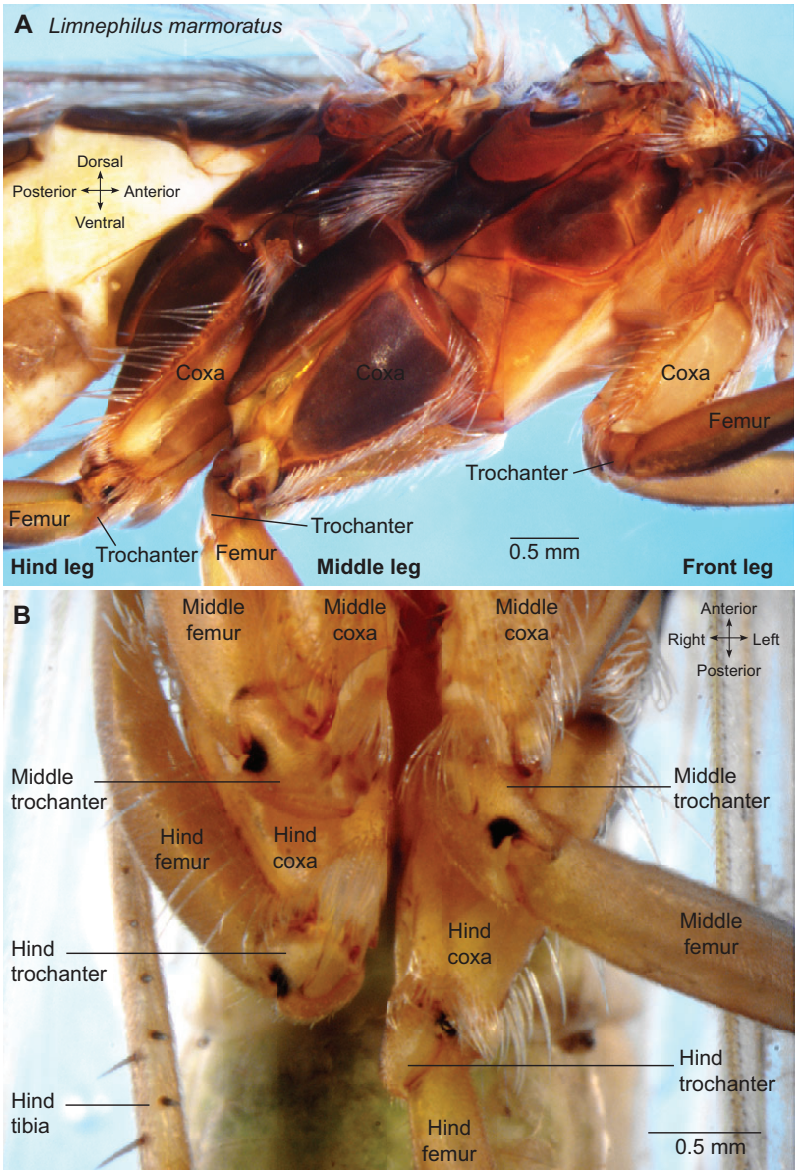

Fig. 2. Proximal joints of the middle and hind legs. (A) Photograph of a side view of the thorax of *L. marmoratus* showing the different orientations of the middle and hind legs. (B) Photograph of a ventral view of the thorax with the right middle and right hind trochantera fully levated about their respective coxae, and the left middle trochantera partially depressed and the left hind trochanter fully depressed.

values are not significantly different across the three species (F=0.401, P=0.671, ANOVA).

At these times the middle legs were only partially depressed and extended so that for the final few milliseconds before take-off a jump was propelled solely by their continuing movement. The loss of contact by the middle legs with the ground defined the time for take-off. At the start of a jump, the tarsi of each of the propulsive legs were in contact with the ground along most of their five segments, but as they depressed and extended, the proximal segments progressively lost contact with the ground so that the most distal segments were the last to leave the ground. The progressive straightening of first the hind legs and then the middle legs gradually raised the body from the ground and because the head end was raised the most, the angle of the body relative to the horizontal was also increased. During all of these movements, the front legs did not move in a consistent way that indicated that they were also contributing to the propulsive force. Moreover, they lost contact with the ground a few milliseconds after the start of the movement of the middle and hind legs. Their role in jumping was thus limited to balancing and perhaps helping to raise the front end of the body during the initial application of thrust by the other four legs.

At the start of a jump the long antennae assumed different positions; for example, they could be raised above the head with the tips pointing forwards (Fig. 3); curved forwards with the distal segments resting on the ground (Fig. 4); or held outstretched in front and with the tips at the same height as the head (Fig. 5). The increasing acceleration during the course of a jump resulted in the antennae being swept backwards from all of these initial starting positions. Throughout the acceleration phase to take-off, the wings remained folded over the body and did not open or begin to flap. Wing movements therefore made no contribution to the forces generating take-off. Similarly, once airborne, the wings remained in this folded position so that they could exert no influence on the jump trajectory. Many jumps continued to a landing without any movements of the wings, while in some, the wings started to open 5–15 ms after take-off and there was a smooth transition to powered, flapping flight.

Second strategy for jumping

In this strategy, the wings opened and then began the first depression movement of the wing beat cycle before the legs lost contact with the ground and the insect became airborne. The two strategies were

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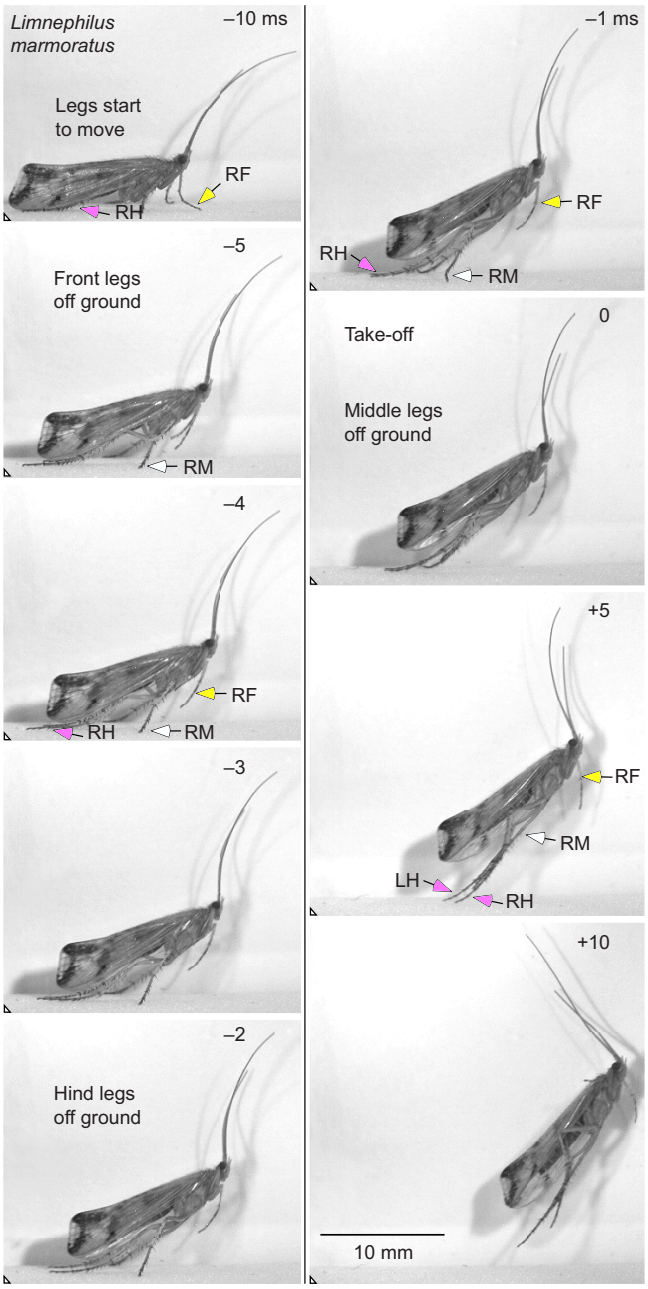

Fig. 3. Jump by *L. marmoratus* in which only the legs participate. The middle and hind legs provided the propulsive force for the jump and raised the front legs from the ground 5 ms before take-off. The hind legs also left the ground before take-off. The following conventions are used here and in Figs 4–8. Selected images, at the times indicated, are arranged in two columns. They were captured at a rate of 1000 images s^{-1} and with an exposure time of 0.2 ms. The front legs (LF, left front; RF, right front) are indicated by arrows with yellow heads, the middle legs (LM, RM) by arrows with white heads and the hind legs (LH, RH) by arrows with pink heads. The triangles in the bottom left-hand corner of each image indicate a constant spatial reference point.

used by the same individual caddis fly on different occasions. There was no indication that one strategy was used preferentially by a particular individual or by any one of the three different species. All jumps were, however, made in the same environment of the chamber but they were generated either apparently spontaneously, or in response to a light touch applied with a probe to the abdomen. The sequence of leg movements was the same as in the first strategy for jumping (Fig. 6). The front legs were the first to leave the ground, followed by the hind legs, after they had reached full depression and extension. Take-off was again defined by the middle legs losing contact with the ground. The details of these leg movements were most clearly revealed when a caddis fly took off from the vertical glass surface of the chamber so that the ventral side of the thorax was visible (Fig. 7). Furthermore, the elevation of the wings meant that they no longer obscured any parts of the legs. At the start of the jump, the femora of the middle and hind legs were drawn forward by levation about the coxae of their respective trochantera and closely linked femora. The femora of the middle legs were close to the ventral surface of the thorax, whilst those of the middle legs were close to the sides of the thorax. The first propulsive movements were depression of the coxo-trochanteral joints accompanied by extension of the femoro-tibial joints. Again, the middle and hind legs were oriented differently; the middle femora projected sideways and the whole legs were directly beneath the middle of the thorax. By contrast, the femora of the hind legs were angled upwards and backwards so that the whole legs projected backwards along the lateral edges of the abdomen. The hind legs were the first to achieve full depression and extension of these joints and thus were the next legs to lose contact with the glass surface. The middle legs then proceeded to depress and extend further and completed their contribution to propulsion when they lost contact and the insect became airborne.

The sequence of wing movements was similar in all the 30 jumps of this strategy that were analysed. The wings were opened and raised above the body before the propulsive movements of the middle and hind legs started (Fig. 8; supplementary material Movie 3). As these leg movements continued, the wings gradually depressed but at take-off had not completed the full extent of their depression movement. Completion was thus delayed until the caddis fly was fully airborne, enabling the wings to avoid possible damage if they were to hit the ground.

Jumping performance

The following features of jumping performance were calculated from measurements made of the three species of caddis fly and from the kinematics of their jumps (Table 1). In this cross-species comparison, mean acceleration time (the time from the first movement of the middle and hind legs until the middle legs lost contact with the ground and the caddis fly became airborne) ranged from 14.5 to 15.4 ms across the three species. These times were not significantly different although the body mass of the heaviest species, *L. marmoratus*, was three times greater than that of *M. angustata* and almost 10 times greater than that of the lightest species, *M. azurea*. Similarly, mean take-off velocity ranged only between 0.7 and 1.0 m s^{-1} across the three species, with the lightest species having the lowest value and the intermediate *M. angustata* having the highest value. *Mystacides azurea* required 1.4 μJ of energy to generate its fastest jumps, while this requirement rose to 6.6 μJ in *M. angustata* and to 29.2 μJ in *L. marmoratus*. In the three species, mean acceleration ranged from 51 to 64 m s^{-2}, mean forces of 5–7 ***g*** were experienced and power output ranged from 0.1 to 1.0 mW. The fastest jumps would require a power output of 226–343 W kg^{-1} of muscle in the different species, assuming that the muscles powering the propulsive movements of the middle and hind legs comprised approximately 10% of body mass, as found in other jumping insects using a single pair of propulsive legs (Burrows, 2006). The use of the two pairs of propulsive legs, and hence the potential doubling of the mass of jumping muscle, suggests that the calculated requirements should be halved.

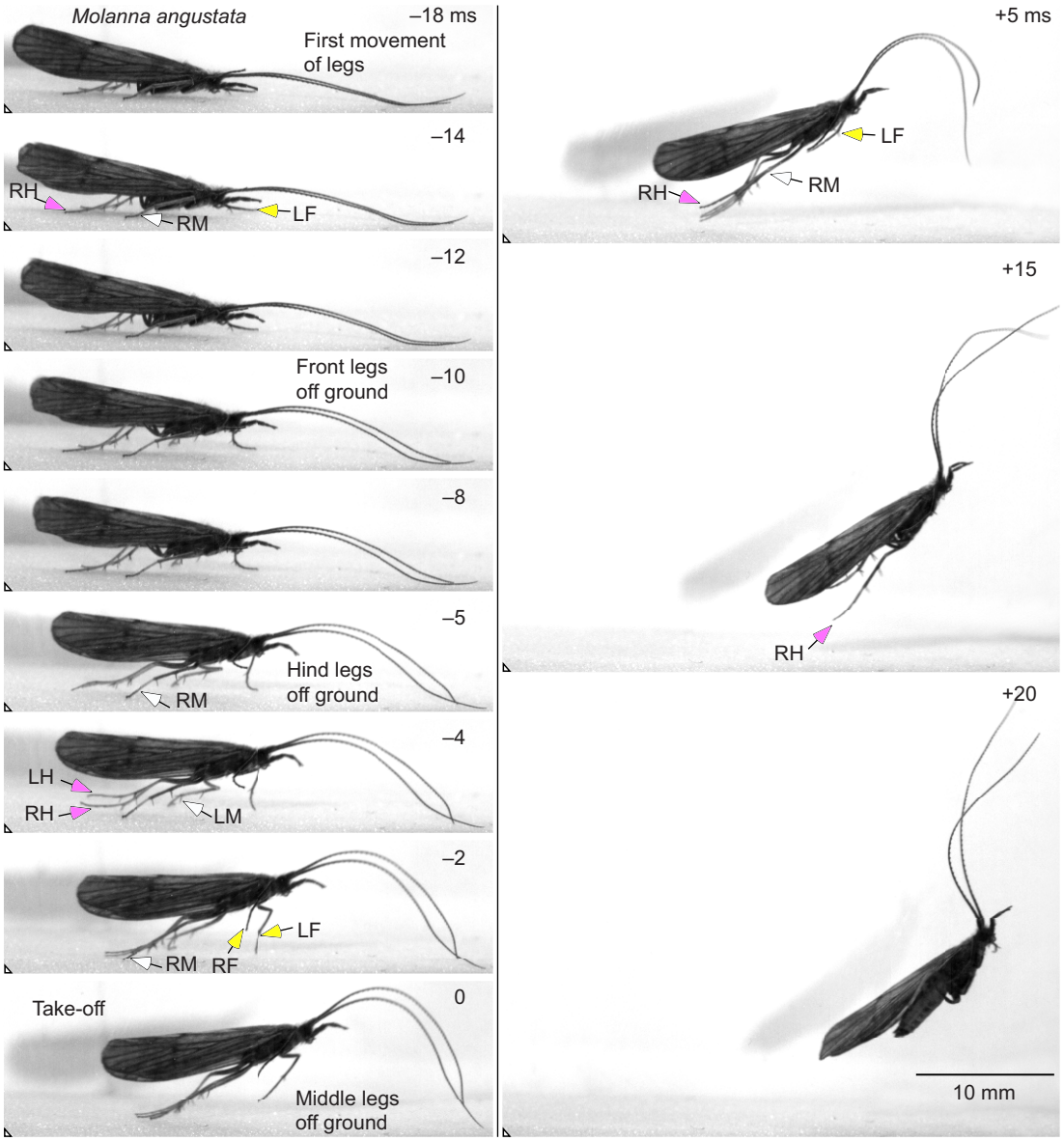

Fig. 4. Jump by *Molanna angustata* propelled only by the legs. Both the middle and hind legs again provided the propulsion for take-off and the wings remained folded and stationary both during the propulsive leg movements and once the insect was airborne.

A comparison of jumping performance was then made for the two different jumping strategies. In the first strategy in which jumps were propelled only by movements of the legs, the angle of the body relative to the horizon at take-off was 9.3±1.9 deg (grand mean of 29 jumps by 9 caddis flies). By contrast, in the second jumping strategy in which the wings also moved before the caddis fly became airborne, the body angle at take-off was 35.3±2.5 deg (grand mean of 19 jumps by 7 caddis flies). These values are significantly different (Student's two-tailed *t*-test assuming equal variance, P=0.000003); moreover, in each insect the mean body angle was always higher for jumps that involved wing movements. In jumps of *L. marmoratus* propelled only by the legs, the acceleration time was 15.7±0.6 ms, the peak take-off velocity was 1.0±0.07 m s^{-1} and the angle of the trajectory was 61.7±6.0 deg. In jumps involving movements of both wings and legs, the comparable figures were 17.5±2.3 ms, 0.9±0.07 m s^{-1} and 45.6±6.5 deg. None of these three pairs of figures were significantly different (P=0.5, 0.5 and 0.2, respectively, Student's two-tailed *t*-test assuming equal variance). The time at which the middle and hind legs left the ground also did not differ between the two strategies for jumping; in the first strategy, when leg movements alone propelled a jump, the mean timing difference across all three species was 3.33±0.29 ms and in the second strategy, when wing movement also occurred, the difference was 3.22±0.37 ms (P=0.808, N=51 and 23 jumps, respectively).

DISCUSSION

This study has shown that adult caddis flies jump by depressing and extending the middle and hind pairs of legs at the same time. The front legs set the angle of the body relative to the substrate but lost contact with the ground as the other legs began their propulsive movements. The hind legs were the next to lose ground contact so that the final thrust to take-off was applied only by the middle legs.

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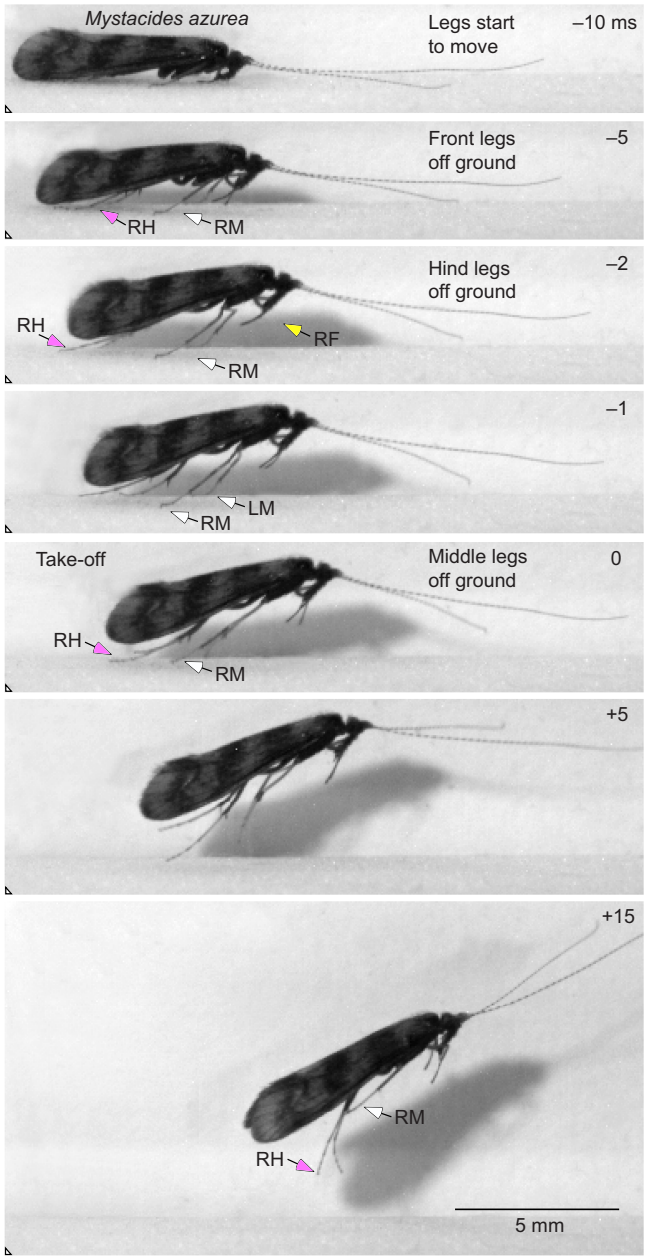

Fig. 5. Jump by *Mystacides azurea*, the smallest caddis fly analysed. A jump that was propelled by movements of the legs alone. The hind legs left the ground 2 ms before take-off.

Use of two pairs of propulsive legs

A number of groups of insects also move both the middle and hind legs together to propel jumping, but the timing of the start of the movement of a particular pair of legs can vary, as can the pair that is the last to leave the ground at take-off (see the diagrammatic representation of the sequences in Fig. 9). Praying mantises (Burrows et al., 2015), snow fleas (Burrows, 2011) and the dolichopodid fly *Hydrophorous alboflorens* (Burrows, 2013) start the movement of both pairs of legs at the same time and take-off is marked by all the legs losing contact with the substrate together. In lacewings (Burrows and Dorosenko, 2014), both pairs of legs start to move at the same time but the middle legs are the first to lose contact with the ground so that the final thrust is applied by the hind legs. In moths, the middle legs are the first to move and the first to lose contact with the ground, so that it is the hind legs that provide the final thrust (Burrows and Dorosenko, 2015). In the caddis flies analysed in this paper, yet another combination of the two pairs of legs was used; both pairs of legs again started to move at the same time but it was the hind legs that lost contact with the ground first, so that the middle legs provided the final thrust to take-off. This was despite the fact that the hind legs are about 20% longer than the middle legs and should thus act as a more effective lever. Within a particular group these sequences are the ones most commonly observed though the time between the start of the movements by the two pairs of legs can vary. Moreover, in mantises, for example, a steep angle adopted by the body relative to the ground at take-off can result in the middle legs losing contact with the ground before the hind legs.

What advantage do these insects gain from using two pairs of legs rather than one? First, distributing ground reaction forces over four tarsi allows caddis flies and moths to jump from delicate leaves or petals of plants, snow fleas to jump from snow (Burrows, 2011) and the fly *H. alboflorens* to jump from the surface of the water (Burrows, 2013). Acceleration times of the jumps are also slower compared with those of insects of a similar mass using a catapult mechanism so that the ground reaction forces are distributed over a longer time as well as area. Second, using two pairs of legs doubles the muscle mass available to generate the power necessary to launch into the air while allowing the legs to remain of similar size. This contrasts with, for example, grasshoppers, which have hind legs that are much larger than the other legs to provide sufficient space to accommodate the requisite muscle mass.

Jumps are propelled by direct muscle contractions

It is notable that, with the possible exception of snow fleas, these groups of insects that use two pairs of legs for propulsion need only use direct muscle contractions to power their jumps. The acceleration time in caddis flies is about 15 ms and the fastest take-off velocity is only 1.1 m s^{-1}, so the power requirements for jumping are well within the contractile limits of normal muscle, which range from 250 to 500 W kg^{-1} muscle (Askew and Marsh, 2002; Ellington, 1985; Josephson, 1993; Weis-Fogh and Alexander, 1977). This mechanism of generating jumping obviates the need to synchronise closely the movements of all the legs and needs no mechanism for releasing the propulsive muscular energy at the same time in all the legs.

Two strategies for jumping

Caddis flies used two strategies for jumping. The first was a strategy found in the majority of jumps in which propulsion was provided only by the rapid movement of the middle and hind pairs of legs, and the wings remained folded along the body. The wings either remained closed until landing or only began to move several milliseconds after take-off so that flapping flight resulted. The second was a strategy in which wing movements began either before or at the same time as movement of the middle and hind legs, so that all these appendages contributed force to take-off. In these jumps, an earlier transition to flapping flight occurred. No difference in performance as judged by the acceleration times, take-off velocities and trajectory once airborne were apparent in these two strategies. There was, however, a significant difference in the body angle relative to the substrate at take-off; the angle was lower in jumps propelled only by the legs as compared with those that involved movements of the wings before take-off. The increased angle of the body in the latter jumps would enable the initial depression of the wings to be completed at, or just after, take-off and thus avoid possible damage to the wings through their potential contact with the substrate.

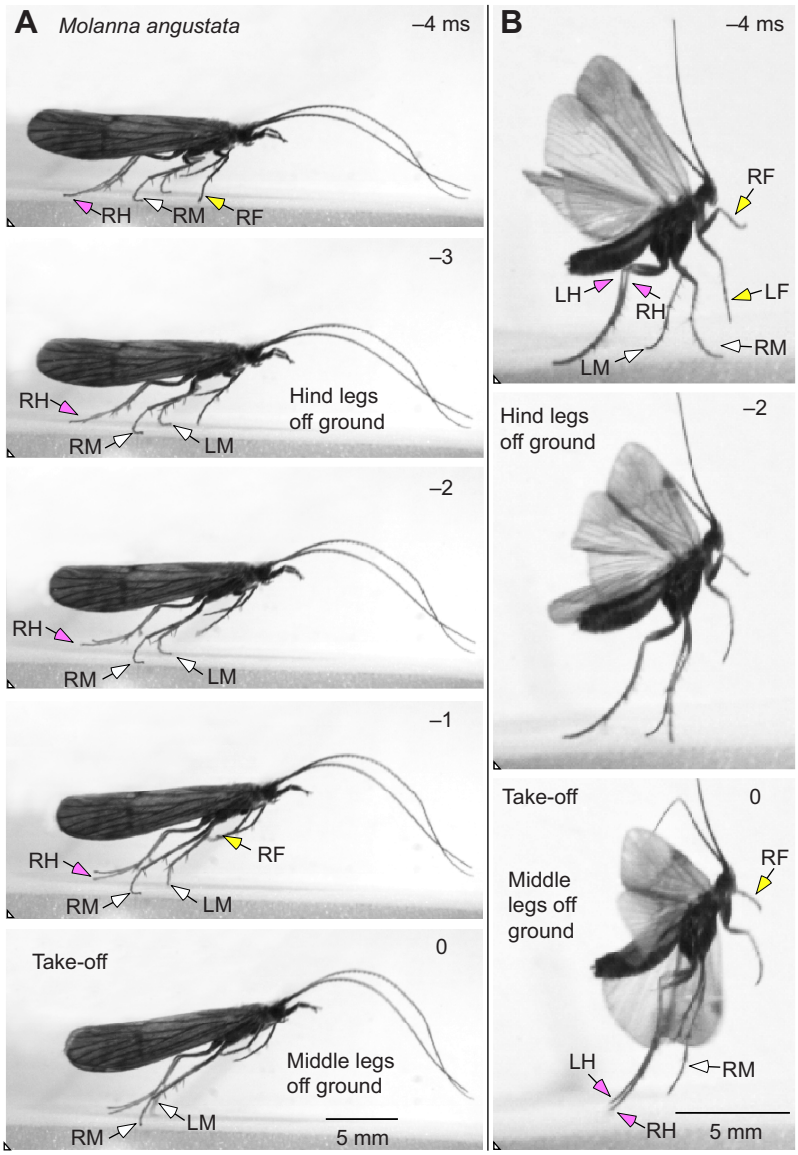

Fig. 6. Details of the leg movements of *M. angustata* in the two jumping strategies. (A) A jump with no movements of the wings. Depression of the coxo-trochanteral and extension of the femoro-tibial joints of the middle and hind legs contributed to propulsion. The hind legs first lost contact with the ground so that take-off occurred when the middle legs left the ground. (B) A jump with movements of the wings. The leg movements follow a similar sequence to that in A with the hind legs losing contact with the ground before the middle legs. The wings were being depressed during these leg movements and before take-off.

The experimental procedure was designed to reveal the kinematics of the movements and hence the mechanism of jumping and not to relate these movements to a variety of behavioural circumstances. Jumps occurred either spontaneously or in response to mild mechanical touch with a fine probe in the confines of a glass chamber. In flies, different strategies for take-off have been associated with different stimuli and different behavioural contexts (Card, 2012). In moths, different jumping strategies have been recognised and analysed but, as in caddis flies, the natural context in which these are used is not known (Burrows and Dorosenko, 2015). There are no previous reports of jumping in caddis flies and thus no indication of how different strategies might be used within their natural environment. The results reported here suggest that jumping could provide a rapid means of locomotion in its own right and of moving rapidly from one location to another. It also provides a means of launching into the air and then transitioning smoothly into flapping flight. The finding that 42% of spontaneous jumps but only 8% of jumps elicited by a mechanical stimulus were accompanied by wing movements suggests that the two jumping strategies described here may be used in different behavioural circumstances. The need is therefore to relate these biomechanical studies more closely to the behaviour of adult caddis flies in their natural habitat during their brief life span.

MATERIALS AND METHODS

Caddis flies, order Trichoptera, were caught in light traps in Girton, Cambridge, UK, and in Llandinam, Powys, UK, during September and October 2012. The species caught fell into three broad categories according to body length and mass: (1) large (body length 10–15 mm and body mass 23–70 mg): *Limnephilus marmoratus* Curtis 1834, cinnamon sedge (family Limnephilae) and *Odontocerum albicorne* (Scopoli 1763), silver sedge (family Odontoceridae), N=22 insects; (2) medium (body length 7–12 mm and body mass 8–16 mg): *Molanna angustata* Curtis 1834 (family Molannidae) and *Oecetis lacustris* (Pictet 1834), longhorn caddis (family Leptoceridae), N=7 insects; and (3) small (body length 4.5–6 mm and body mass 1.5–6 mg): *Mystacides azurea* (Linnaeus 1761), silverhorn (family Leptoceridae), N=26 insects. No video data on *Odontocerum albicorne* and *Oecetis lacustris* are presented.

Photographs of live caddis flies were taken with a Nikon D90 camera fitted with a 100 mm Nikon macro lens. The anatomy of the legs was

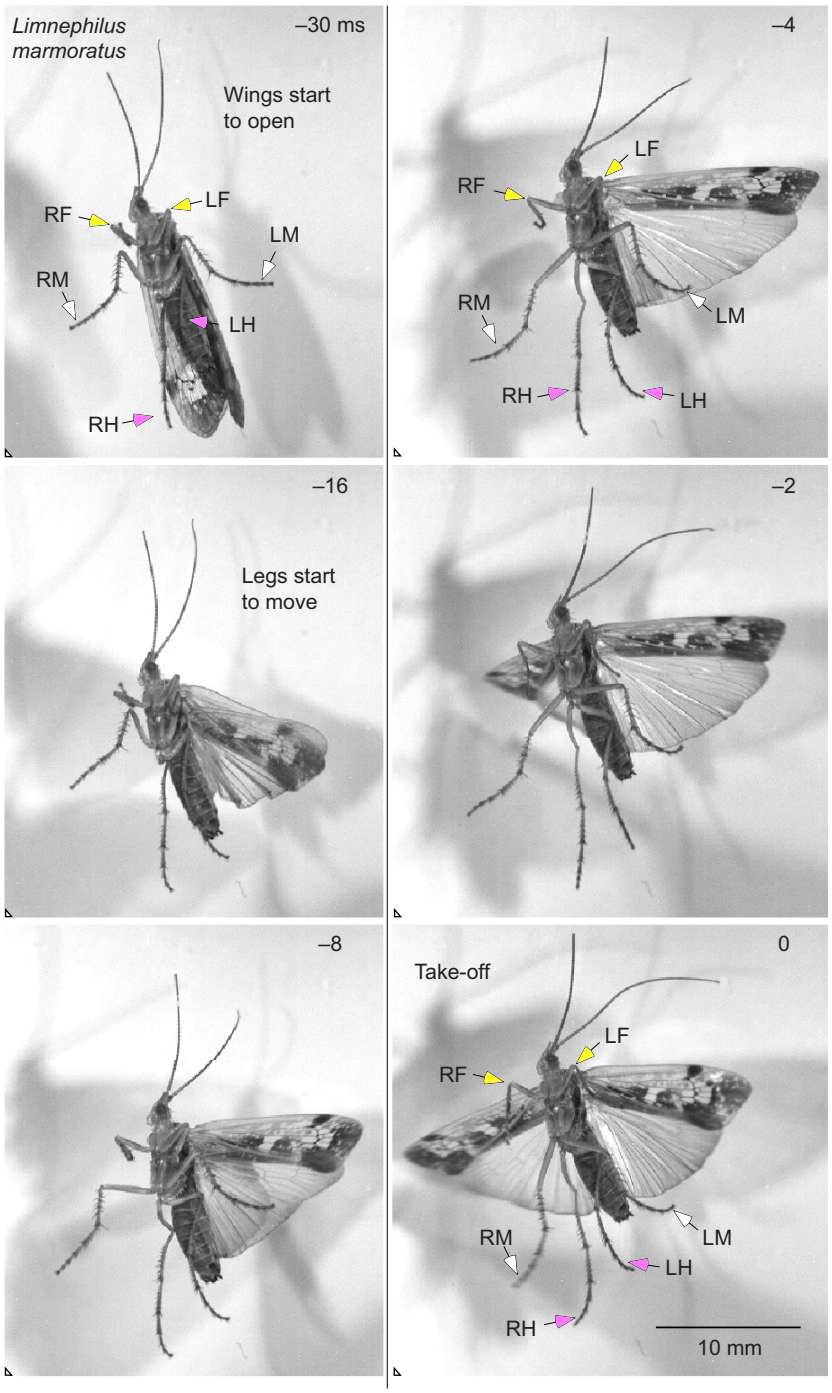

Fig. 7. Jump by *L. marmoratus* viewed from underneath. Both middle legs and both hind legs moved together but the hind legs were the first to lose contact with the glass surface. In this jump, the wings opened and then were being depressed before take-off.

examined in intact caddis flies, and in those fixed and stored in 70% alcohol or 50% glycerol. To determine the lengths of the legs, enlarged images of fixed specimens were captured with a Nikon DXM1200 digital camera attached to a Leica MZ16 microscope (Wetzlar, Germany) and projected onto a large monitor. Images of individual leg segments (trochanter, femur, tibia and tarsus) were then measured against a ruler and the sum of these parts gave the length of a particular leg to an accuracy of 0.1 mm. Body masses were determined to an accuracy of 0.1 mg with a Mettler Toledo AB104 balance (Beaumont Leys, Leicester, UK).

Analyses of jumping behaviour were based on 90 jumps by 12 caddis flies; eight *L. marmoratus*, two *M. angustata* and two *M. azurea*. Each individual produced a minimum of five jumps and means were derived to describe their performance. Grand means±s.e.m. are given for each species. Sequential images of jumps were captured at rates of 1000 frames s^{-1} and an exposure time of 0.2 ms, with a single Photron Fastcam SA3 camera [Photron (Europe) Ltd, High Wycombe, Bucks, UK], fitted with a 100 mm micro Tokina lens. The images were fed directly to a computer for later analysis. Of the 90 jumps recorded, 59% occurred spontaneously while the remaining 41% were elicited in response to a mechanical stimulus. The jumps were performed in a chamber made of optical quality glass that was 80 mm wide, 80 mm high and 25 mm deep. The floor, side walls and ceiling were made of high density foam (Plastazote, Watkins and Doncaster, Cranbrook, Kent, UK) to give traction at take-off. The caddis flies would jump from any of these surfaces. The camera pointed directly at the middle of the glass face at the front of this chamber. Measurements of changes in joint angle and distance moved were made from jumps that were as close as possible parallel to the image plane of the camera. Jumps that deviated from the image plane of the camera by less than ±30 deg were calculated to result in a maximum error of 10% in the

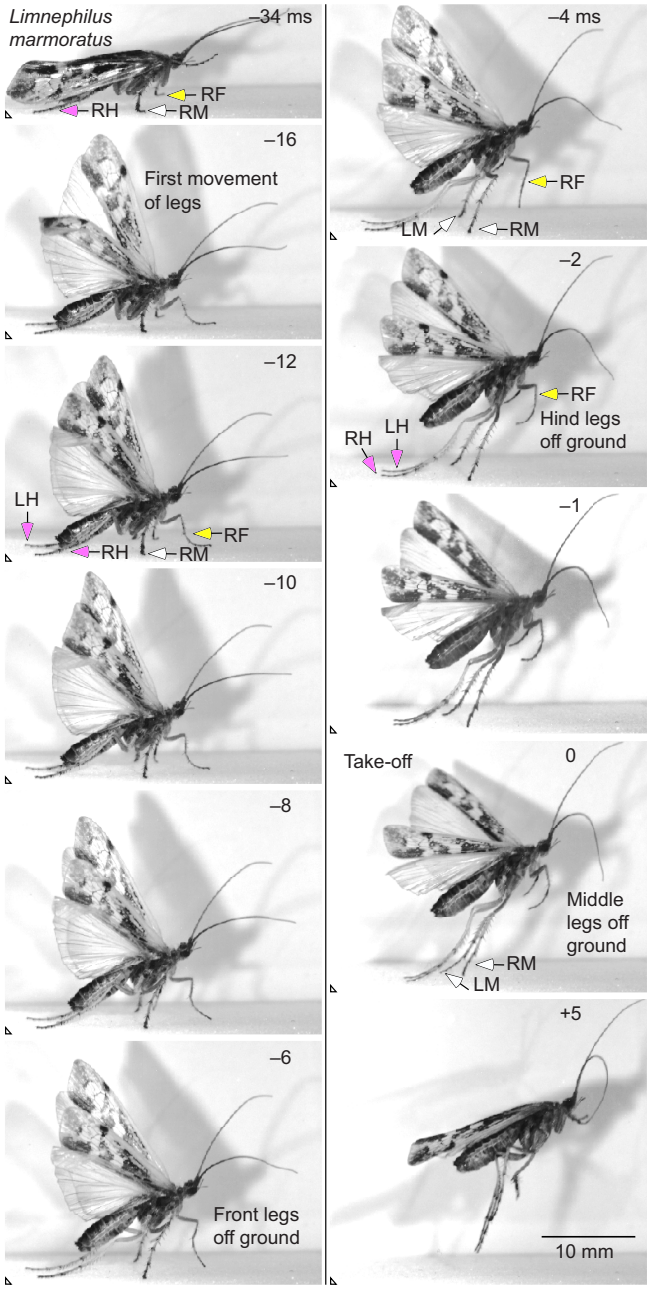

Fig. 8. Wing and leg movements in a jump by *L. marmoratus* as viewed from the side. The wings opened before any propulsive movements of the middle or hind legs started. During the leg movements, the wings were depressed and at take-off had not completed the depression phase of their first cycle of a wingbeat.

measurements of joint or body angle. Selected image files were analysed with Motionscope camera software (Redlake Imaging, Tucson, AZ, USA) or with Canvas 14 (ACD Systems International, Seattle, WA, USA). The time at which the middle pair of legs lost contact with the ground and the insect became airborne (take-off) was designated as time t=0 ms so that different jumps could be aligned and compared. The time from the first detectable movement of the middle and hind legs until take-off defined the acceleration period of a jump. An error of one frame in estimating the first movement of the hind legs or the take-off time would result in a 10% error in measuring acceleration time. Peak velocity was calculated as the distance moved in a rolling 3-point average of successive images before take-off. A point on the body that could be recognised in successive frames and was close to the centre of mass was selected for measurements of the trajectory of the caddis

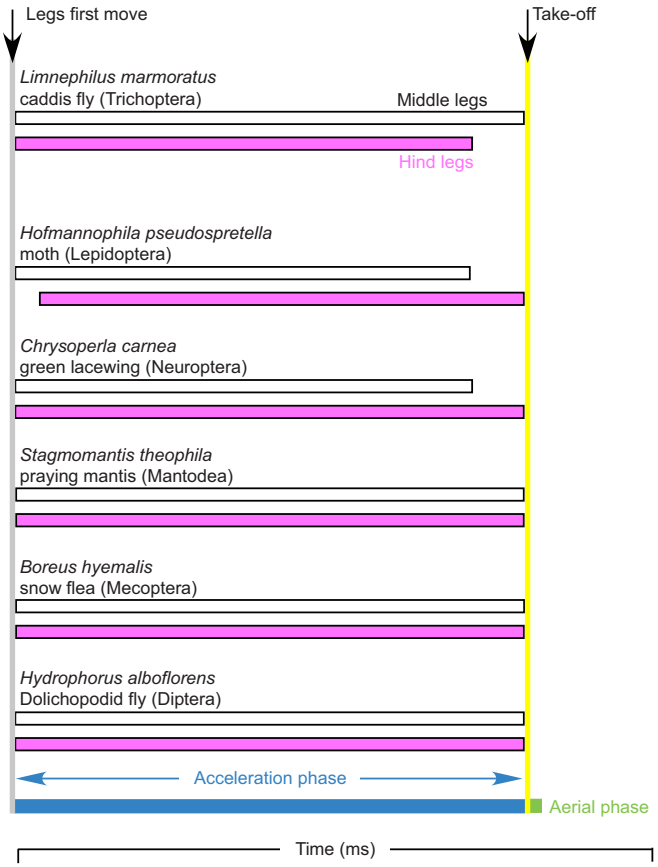

Fig. 9. Diagrammatic representation of the sequence of jumping movements of the middle and hind legs in six orders of insects. The movement of the middle legs (open horizontal bars) and hind legs (pink horizontal bars) is indicated during the acceleration phase of a jump relative to the start of the first propulsive movements (vertical grey bar) and take-off (vertical yellow bar).

fly after take-off. The angle subtended by a line joining these initial positions after take-off, relative to the horizontal, gave the trajectory angle. The body angle at take-off was defined as the angle subtended by the longitudinal axis of the caddis fly relative to the horizontal at the point of take-off. Temperatures ranged from 22 to 25°C.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
The authors contributed equally to all aspects of the experimental work and the analyses.

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