

RESEARCH ARTICLE

Jumping mechanisms in lacewings (Neuroptera, Chrysopidae and Hemerobiidae)

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ABSTRACT

Lacewings launch themselves into the air by simultaneous propulsive movements of the middle and hind legs as revealed in video images captured at a rate of 1000 s⁻¹. These movements were powered largely by thoracic trochanteral depressor muscles but did not start from a particular preset position of these legs. Ridges on the lateral sides of the meso- and metathorax fluoresced bright blue when illuminated with ultraviolet light, suggesting the presence of the elastic protein resilin. The middle and hind legs were longer than the front legs but their femora and tibiae were narrow tubes of similar diameter. Jumps were of two types. First, those in which the body was oriented almost parallel to the ground (−7±8 deg in green lacewings, 13.7±7 deg in brown lacewings) at take-off and remained stable once animals were airborne. The wings did not move until 5 ms after take-off when flapping flight ensued. Second, were jumps in which the head pointed downwards at take-off (green lacewings, −37±3 deg; brown lacewings, −35±4 deg) and the body rotated in the pitch plane once airborne without the wings opening. The larger green lacewings (mass 9 mg, body length 10.3 mm) took 15 ms and the smaller brown lacewings (3.6 mg and 5.3 mm) 9 ms to accelerate the body to mean take-off velocities of 0.6 and 0.5 m s⁻¹. During their fastest jumps green and brown lacewings experienced accelerations of 5.5 or 6.3 g, respectively. They required an energy expenditure of 5.6 or 0.7 μJ, a power output of 0.3 or 0.1 mW and exerted a force of 0.6 or 0.2 mN. The required power was well within the maximum active contractile limit of normal muscle, so that jumping could be produced by direct muscle contractions without a power amplification mechanism or an energy store.

KEY WORDS: Biomechanics, Kinematics, Flying, Escape movements

INTRODUCTION

Most insects that jump are propelled by a single pair of legs that move together rapidly and powerfully. There are exceptions, however, such as the springtails (Collembola), which use the fast extension of an abdominal appendage (Brackenbury and Hunt, 1993; Christian, 1978; Christian, 1979) and click beetles which use the rapid movement of the joint between the pro- and mesothorax (Evans, 1972; Evans, 1973; Kaschek, 1984). Most commonly it is the single pair of hind legs that propels jumping, although in small flies such as *Drosophila*, it is the middle pair of legs (Card and Dickinson, 2008; Zumstein et al., 2004). In some other dipteran flies and snow fleas (Mecoptera) (Burrows, 2011) two pairs of legs, the hind and the middle, are moved together. Synchronizing four legs

increases the complexity of muscle control but has the advantage of increasing the muscle mass that can be devoted to jumping while avoiding the specialisation in shape and size of the legs. In snow fleas it also allows four energy stores – one for each leg – to be used in its catapult jumping action (Burrows, 2011). Furthermore, by distributing ground reaction forces over a larger surface area, take-off becomes possible from more compliant surfaces. For the fly *Hydrophorus albofloreus* this even enables jumping from the surface of water by ensuring that the legs do not penetrate the surface (Burrows, 2013a).

In all jumping movements, the same demands exist for high take-off velocities and short acceleration times, particularly when escape is the required outcome. If the propulsive legs are short then these conflicting demands can be met only by the use of a catapult mechanism that allows the power-producing muscles to contract slowly and store energy in distortions of the skeleton, which can then be released suddenly to power the jump. Such a mechanism is used by a variety of insects, including locusts (Orthoptera), plant-sucking bugs (Hemiptera) and fleas (Siphonaptera) (Bennet-Clark, 1975; Bennet-Clark and Lucey, 1967; Burrows, 2006a; Burrows, 2006b; Burrows, 2007b). An alternative mechanism is to use direct contractions of the muscles to power the propulsive movements of the legs. This will generate slower movements of the legs and slower take-off velocities even if leverage is increased by the use of long hind legs as in bush crickets (Burrows and Morris, 2003).

Lacewings (Neuroptera) are agile insects with large diaphanous wings and legs that are shorter than their body. They nevertheless move rapidly around woody shrubs and trees, particularly after dusk, and frequently launch into flight. This paper analyses whether jumping plays a role in these fast movements and particularly in enabling rapid take-off. It also seeks to determine what combinations of legs might be used and whether their movements are powered by direct muscle contractions or are used in a catapult mechanism. To answer these questions, the legs were therefore examined anatomically and their movements during take-off were analysed by high-speed imaging.

RESULTS**Body shape**

The appearance of lacewings was dominated by their large wings and by their long antennae that were 75% of body length and were normally held pointing upwards and forwards (Fig. 1A–C). The green lacewings (*Chrysoperla carnea* group) had a mass of 9.0±1.1 mg (mean ± s.e.m.) and a body length of 10.3±0.4 mm and were thus heavier and larger than the brown species *Micromus variegatus* which had a mass of 3.6±0.4 mg and a body length of 5.3±0.3 mm (*N*=7 for each species) (Table 1). The values are significantly different both for the masses (*t*-test: *t*₁₀=4.49, *P*=0.001) and the body lengths (*t*-test: *t*₁₀=11.17, *P*<0.0001). The translucent wings increased the overall length of green lacewings by 30±2.4% and the mottled wings of the two brown species (*Micromus*

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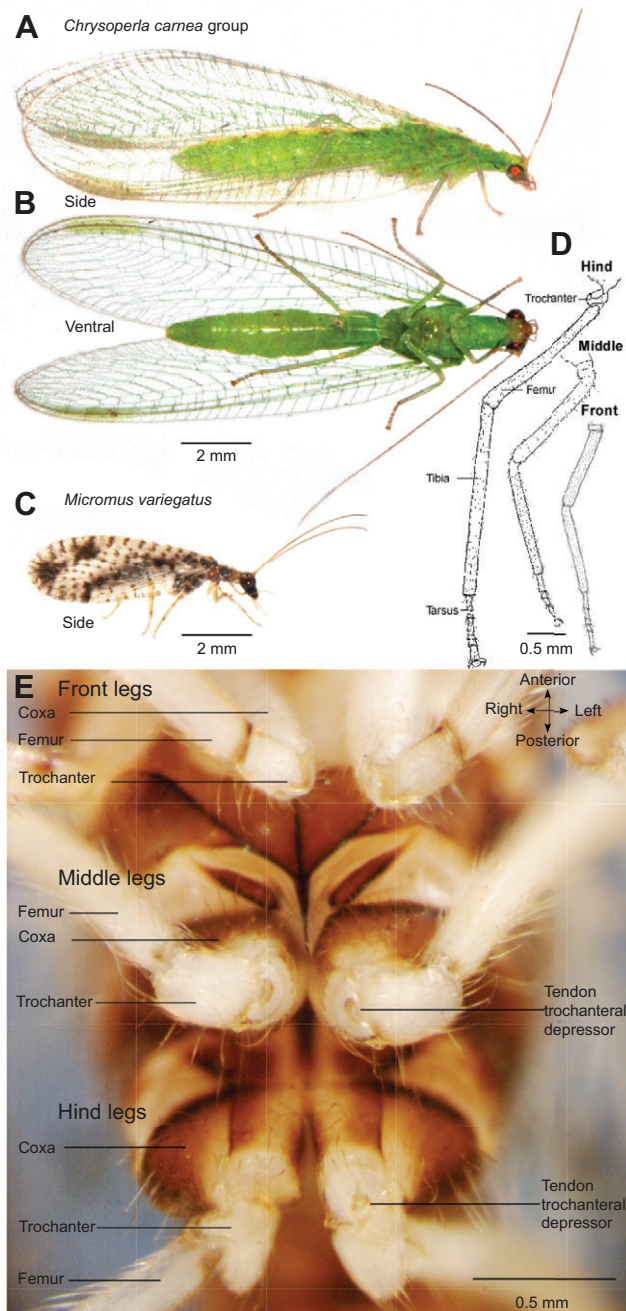


Fig. 1. Shape of the body and legs of two species of lacewings analysed. (A) Side view of an adult green lacewing that belongs to the *Chrysoperla carnea* group. (B) Ventral view of the same insect. (C) Side view of an adult of the smaller brown lacewing *Micromus variegatus*. (D) Drawings to show the relative proportions of the front, middle and hind legs of a green lacewing. (E) Photograph of a ventral view of the thorax of a brown lacewing. The hind trochanters are partially depressed and the middle trochanters are levated.

variegatus and *Hemerobius humulinus*) by $55 \pm 4.5\%$. The wings also extended above and below the body when folded.

The middle legs of green lacewings were 20% longer and the hind legs were 70% longer than the front legs so that the ratio of leg lengths was 1:1.2:1.7 (front: middle: hind) (Fig. 1D; Table 1). In brown lacewings, the middle legs were 50% longer and the hind legs were 110% longer than the front legs giving a ratio of 1:1.5:2.1. The increased length of the hind legs in the different species can be

attributed to their longer femora and tibiae (Table 1). The hind legs of green lacewings were 55% of body length compared with 70% in the brown ones. Relative to the cube root of body mass, green and brown lacewings had ratios of 2.7 and 2.5, respectively.

The orientation of legs was such that the hind legs moved close to the lateral surfaces of the abdomen with a femur pointing backwards and when flexed the femoro-tibial joint was above the dorsal surface of the abdomen (Fig. 1A, Fig. 3). The middle and front legs extended more laterally so that the tarsi were placed away from the edges of the body with femora pointing almost horizontally and forwards (Fig. 1B, Fig. 3). The coxae of the middle and hind legs were large and closely apposed at the ventral midline (Fig. 1E). The trochanters were short and were able to rotate through ~ 100 deg about their respective coxae. They were depressed or levated by muscles within the thorax. The depressor tendon was particularly large and was clearly visible through the flexible joint membrane at its insertion on the medial, ventral rim of a trochanter (Fig. 1E). The front legs were the shortest of all three pairs of legs and were held with the femora pointing forwards and close to the prothorax. The front coxae were more widely separated from each other at the ventral midline and were more elongated than those of the middle or hind legs (Fig. 1E, Fig. 2A). The femora and tibiae of all three pairs of legs were long thin tubes with a consistent diameter along their whole length. This shape of the femora in particular indicates that large muscles capable of generating powerful extensions of the tibiae were absent. The five segmented tarsi ended in curved claws.

In both green and brown lacewings, the lateral walls of the meso and metathoracic segments each had a prominent ridge toward their posterior edges that extended from the hinges of the front or hind wings, respectively, to the articulation of the coxae (Fig. 2A). When the thorax was illuminated with UV light (see the Materials and methods for details of wavelengths), these ridges showed a bright blue fluorescence when viewed from the outer surface, suggesting the presence of resilin (Fig. 2B,C). When soft internal tissue had been removed, the blue fluorescence was also visible from the inner surfaces (Fig. 2D,E).

Kinematics of the jump

Jumps by both green and brown lacewings were propelled by the combined actions of the middle and hind legs. No changes in the joint angles of the front legs could be related to any direct propulsive actions. Furthermore, the wings did not open or begin to flap until the lacewing had been airborne for at least 5 ms and could not therefore have contributed any force to a jump before this time. Two broad categories of jumps could be distinguished from the 115 jumps by 17 lacewings that were analysed. First were jumps in which the longitudinal body axis remained stable, particularly in the pitch plane (Figs 3–5; supplementary material Movies 1 and 2). The wings opened once airborne and flapping flight then followed. In green lacewings 59% (65% in brown lacewings) of jumps were in this category. Second, were jumps in which the body pitched forwards during take-off and continued rotating once airborne (Figs 5–7; supplementary material Movie 3). In green lacewings 41% (35% in brown lacewings) of jumps were in this category. In just one of these jumps by a green lacewing and one jump by a brown lacewing did the wings open and flap once airborne, but the body orientation remained unstable and the insect crashed.

The sequence of leg movements was essentially the same in all jumps but will be described first for those in which the orientation of the body remained stable. Propulsive movements in both green

Table 1. Body form of green and brown lacewings

	Body mass (mg)	Body length (mm)	Hind leg, femur (mm)	Hind leg, tibia (mm)	Ratio of leg lengths			Hind leg length	
					Front	Middle	Hind	% of body length	Length (mm)/body mass ^{1/3} (mg)
Green lacewing (<i>N</i> =7) <i>Chrysoperla carnea</i> group	9.0±1.1	10.3±0.4	1.9±0.1	2.6±0.1	1	1.2	1.7	55	2.7
Brown lacewing (<i>N</i> =7) <i>Micromus variegatus</i>	3.6±0.4	5.3±0.3	1.1±0.1	1.6±0.1	1	1.5	2.1	70	2.5

Body mass and length, and lengths of the hind femora and tibiae are means ± s.e.m. The ratio of leg lengths is given relative to the front legs; *N* indicates the number of individuals from which the measurements were taken. The values in the two right-hand columns are calculated from the mean values given in four left columns.

(Fig. 3) and brown (Fig. 4) lacewings began from a posture in which the hind and middle legs were levated at their coxo-trochanteral joints, but not necessarily to their maximal extent. Similarly, the middle and hind tibiae were not fully flexed about their femora, but instead typically adopted an angle of ~90 deg. This implies that neither locking of a trochanter about a coxa by full levation, or a tibia about a femur by full flexion were essential prerequisites of jumping. From this initial posture, the first propulsive movements were a depression of both hind and both middle trochantera about their respective coxae that occurred within 1 ms of each other (Fig. 5A,B). In side views of the lacewing, these movements were most apparent as a change in the angle of a femur relative to the body, because each small trochanter was closely attached to a femur. The tibiae also began to extend at the same time, but after a small extension movement the middle tibiae then flexed through a few degrees while the hind tibiae continued to extend. The progressive depression of the trochantera and the extension of the tibiae gradually raised the body and this had two consequences; first the short front legs lost contact with the ground 4–6 ms before take-off; second, once the middle legs were fully outstretched by reaching maximal depression and extension, they also lost contact with the ground. These timings varied by a few milliseconds but showed clearly that thrust was initially applied by the two hind and two middle legs and that for the final few milliseconds was applied only by the hind legs. The hind legs continued to depress and extend, propelling the lacewing upwards and forwards, until they too reached the full extent of their movements by becoming fully outstretched. At this point the tips of the hind tarsi lost contact with the ground and the lacewing became airborne. The body angle at take-off was -7 ± 8 deg (mean of 22 jumps by eight green lacewings) and 13.7 ± 7 deg (mean of 23 jumps by nine brown lacewings). The angle of the body was thus on average a few degrees either side of horizontal, but there was large variation between different jumps with the head pointing upwards more often than downwards without a discernible effect on the stability of a jump.

The wings remained closed and did not move throughout this acceleration phase of the jump (the time from the first propulsive movements of the middle and hind legs until the loss of ground contact by the hind tarsi). The wings first opened and started to flap a few milliseconds after take-off, so that such jumps led directly to flight. The exception to this opening of the wings occurred in those jumps where a landing site was encountered soon after take-off. A jump from the ground was thus entirely propelled by the movements of the middle and hind legs.

In the second category of jumps by both green (Fig. 6) and brown (Fig. 7) lacewings the body pitched downwards during the propulsive phase and once airborne continued to rotate at a maximum rate of 22 Hz. The body angle at take-off relative to the horizontal (head pointing downwards) was -37 ± 3 deg in green

lacewings and -35 ± 4 deg in brown ones. These body angles adopted in the second category of unstable jumps were statistically significantly different from those adopted by either green (*t*-test: $t_{19}=3.65$, $P=0.002$) or brown (*t*-test: $t_{20}=4.04$, $P=0.001$) lacewings in the first category of stable jumps. Pooling all the data for green and brown lacewings in both the more stable jumps and the less stable ones showed a correlation between the angle of body at take-off and the angular rotation of the body relative to the horizontal during the first 10 ms of the airborne trajectory. The more the head pointed downwards and thus the more negative the angle it subtended relative to the horizontal, the greater was the angular rotation. Similarly, if the head pointed upwards, the smaller was the angular rotation.

The contrast between these stable and unstable jumps was most clearly seen when movements of the head and the tip of the abdomen were plotted in the *x* and *y* coordinates (Fig. 8A,C), or against time (Fig. 8B,D). In stable jumps the head moved progressively upwards and forwards while the movements of the abdomen were affected by the elevation and depression of the wings once airborne; as the wings were elevated, the upward displacement of the abdomen slowed only to increase again as the wings were depressed (Fig. 8A,B). During jumps in which the body rotated in the pitch plane the wings remained folded so that it was the propulsive movements of the legs while in contact with the ground that were responsible for the trajectory (Fig. 8C,D).

Jumping performance

An analysis of all the jumps by the green and brown lacewings enabled the following aspects of performance to be calculated (Table 2). The mean acceleration time for green lacewings was 15.2 ± 0.9 ms (*N*=8) and 9.3 ± 0.2 ms (*N*=9) taken by the brown lacewings. The times are statistically significantly different (*t*-test: $t_{15}=6.70$, $P<0.0001$) and the 1.6 times difference can be attributed to the longer time that it takes to accelerate the 2.5 times heavier body mass of the green lacewings. Similar take-off velocities were achieved by green lacewings (0.6 ± 0.04 m s⁻¹) and brown ones (0.5 ± 0.01 m s⁻¹). These means barely reach levels of statistical significance (*t*-test: $t_{15}=2.25$, $P=0.040$), but an individual green lacewing did achieve the highest take-off velocity of 1 m s⁻¹, a value not observed in an individual brown lacewing. Mean accelerations of 39 m s⁻² were reached in the heavier green lacewings rising to 55 m s⁻² in the lighter brown lacewings. In their fastest jumps the green lacewings experienced a force of 5.5 *g* and the brown lacewings a force of 6.3 *g*. The energy required to generate the fastest jumps ranged from 5.6 μJ in green lacewings to 0.7 μJ in brown lacewings. On the basis that the trochanteral depressor muscles of the two hind legs constitutes ~10% of body mass, as found in other jumping insects (Burrows, 2006a), the fastest jump would require a power output of only 274 W kg⁻¹. This value would

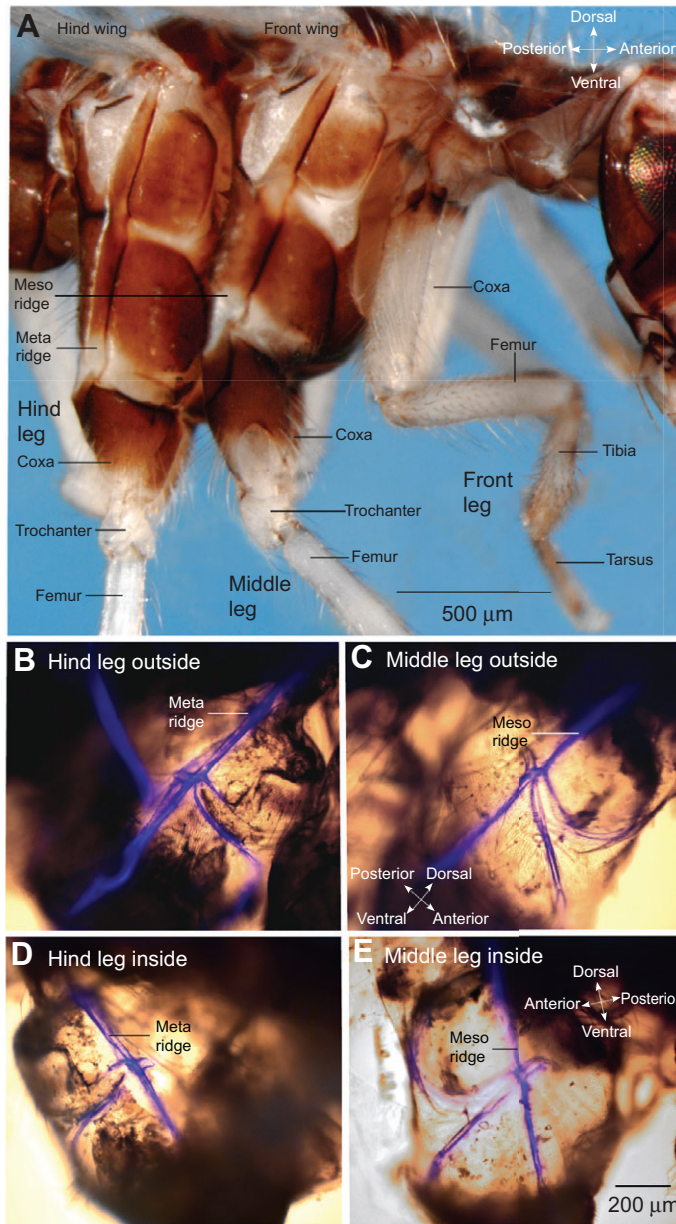


Fig. 2. Thoracic structure and the presence of resilin in the brown lacewing *Micromus variegatus*. (A) Photograph of a lateral view of the right side of the thorax. The proximal parts of the middle and hind legs are of similar shape, but the front coxa is narrower and more elongated. Prominent ridges run from the coxae to the wing hinges on both the meso- and metathoracic segments. (B–E) Blue fluorescence visible on both the outer (B,C) and inner (D,E) surfaces of the thorax of a green lacewing under UV illumination. The diagonal lines of blue fluorescence correspond to the meso- and metathoracic ridges in A. Note the arrows indicating the orientation of each row of photographs.

be halved if the muscles of the middle legs were of similar mass and contributed an equal amount.

The trajectories of jumps had a mean angle relative to the horizontal of 94±10 deg in green lacewings and 95±7 deg in brown ones (values not statistically significantly different), so that most were almost vertical with some even moving slightly backwards. The distance and height generated by stable jumps were not measured because of the intervention of flapping flight soon after take-off. Estimates of the distance (*s*) and height (*h*) that could be

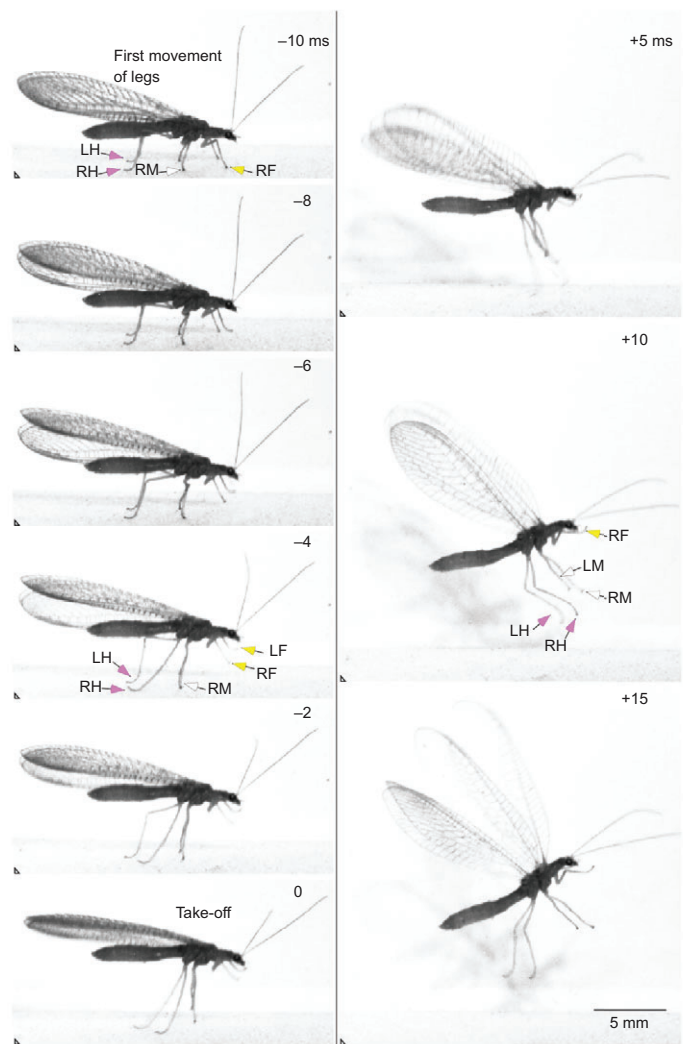


Fig. 3. Jump by a green lacewing of the *Chrysoperla carnea* group. Selected images from a jump captured at a rate of 1000 images s⁻¹ are arranged in two columns. They show the progressive movements of the propulsive middle and hind legs from their beginning until take-off at time 0 ms. Wing movements began only when the lacewing was airborne and then led to flapping flight. 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. The same conventions are followed in Figs 4,6,7.

reached, if a jump provided the only propulsion, were made according to Eqns 1 and 2 below, which describe the motion of an inert body (Alexander, 1968):

$$s = v \cos \Theta \left(\frac{2v \sin \Theta}{9.81} \right), \quad (1)$$

$$h = \frac{(v \sin \Theta)^2}{2 \times 9.81}, \quad (2)$$

where *v* is the velocity at take-off and Θ is the take-off angle.

On this basis, a jump is predicted to propel a green lacewing to a height of 18 mm, or approximately twice its body length and a brown lacewing to a height of 13 mm, or 2.5 body lengths. Forward or backward distances would be only 4–5 mm from take-off angles close

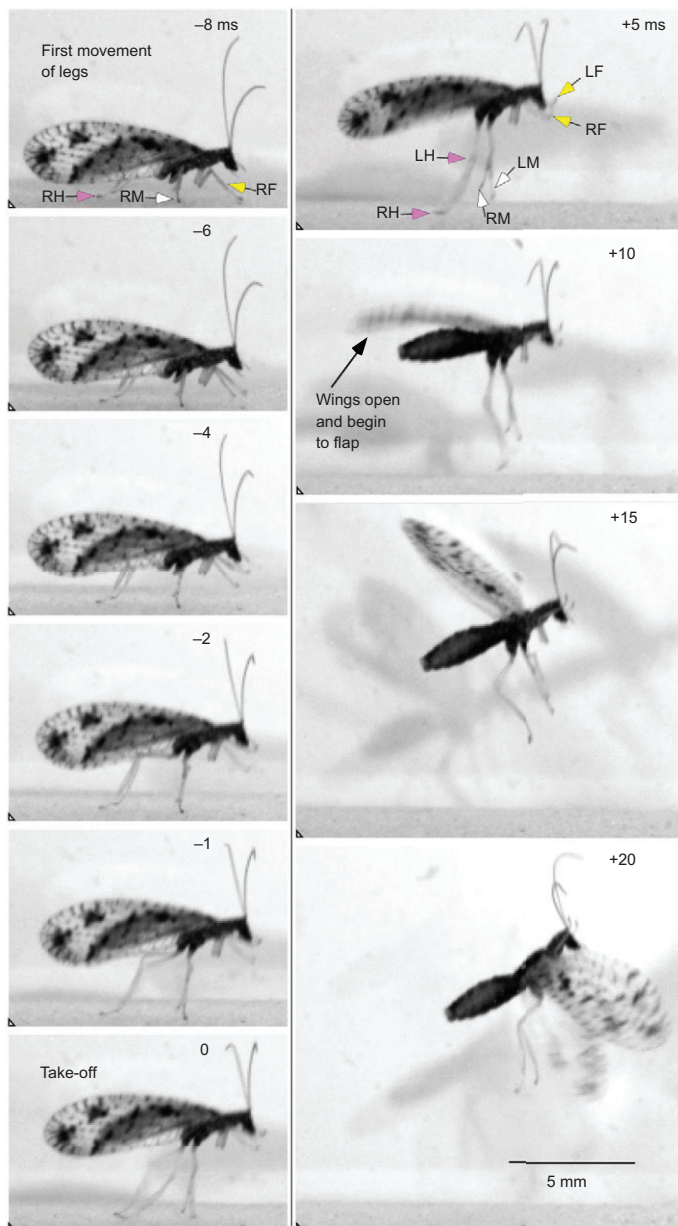


Fig. 4. Jump by a brown lacewing *Micromus variegatus*. The body did not rotate during the movements of the middle and hind legs that propelled take-off. The wings began to open 10 ms after take-off with flapping flight ensuing and the body remaining stable.

to 90 deg relative to the horizontal. The effect of wind resistance is not considered in these estimates. Natural jumps thus favour greater height at the expense of forward (or backward) distance.

DISCUSSION

This paper shows that both green and brown lacewings propel their jumps by the simultaneous movements of the middle and hind pairs of legs. The forces generated could be produced by the direct contraction of the leg muscles without the use of complex mechanisms to store the energy of the muscle contractions.

Power output for jumping

Calculations from the kinematic analyses indicate that jumping requires power outputs no greater than 192 W kg^{-1} by brown

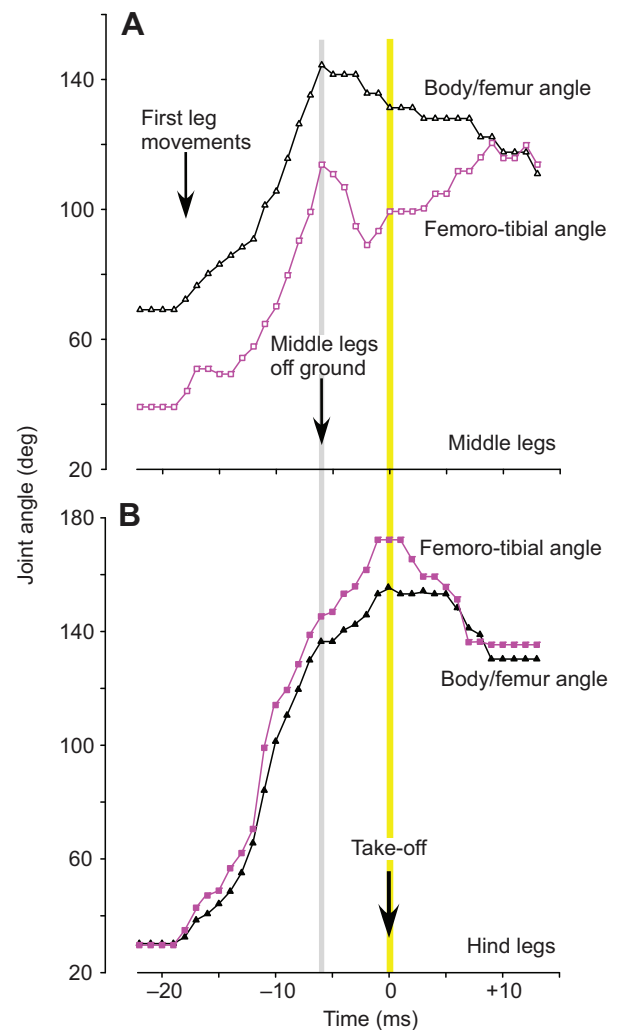


Fig. 5. Angular changes of middle and hind leg joints during a jump by a green lacewing. (A) Plot of the time course of changes in the angle between the body and femur (representing changes in the coxo-trochanteral angle; black open triangles), and the femoro-tibial angles (pink open squares) in the right middle leg. (B) The same angles in the right hind leg are represented by filled symbols. The vertical grey bars indicate when the legs first started to move and when the middle legs lost contact with the ground. The yellow bar shows when the lacewing became airborne at take-off.

lacewings and 274 W kg^{-1} by the heavier green lacewings, even in their best jumps. Such outputs are well within the active contractile capabilities of 250 to 500 W kg^{-1} found for normal muscle from a range of different animals (Askew and Marsh, 2002; Ellington, 1985; Josephson, 1993; Weis-Fogh and Alexander, 1977). This implies that jumping by lacewings could be produced by the direct contraction of the power-producing trochanteral muscles located within the thorax. Some additional power may also be generated by the extensor tibiae muscles, but the thin tube-like shape of the femora indicates that there is limited space available to accommodate much muscle mass. A jump started with the coxo-trochanteral or femoro-tibial joints of the propulsive middle and hind legs held at a range of different angles. This suggests that moving these joints into a position at which locking mechanisms could be engaged to allow muscle contractions to generate and store energy before the legs moved rapidly, as in a catapult mechanism, is not a pre-requisite for jumping. Although there is no requirement for energy storage, however, the sides of the meso- and metathorax have

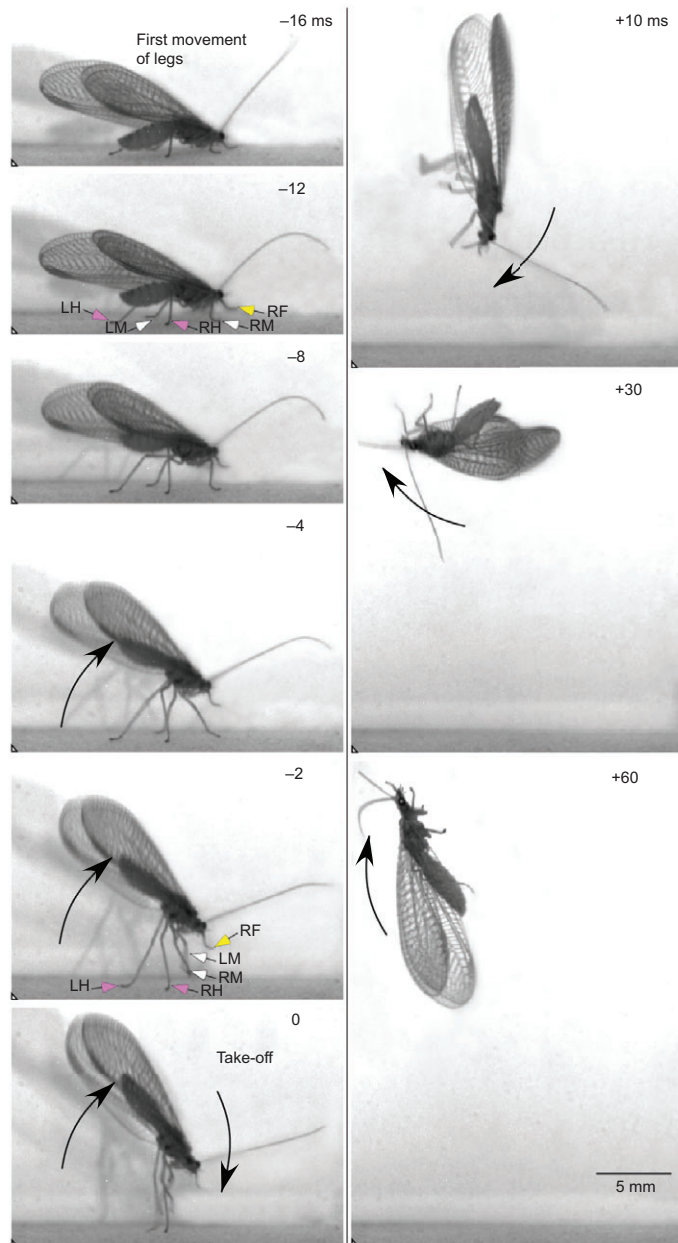


Fig. 6. Jump by a green lacewing in which the body rotated in the pitch plane. A downward pitch of the head (direction indicated by black arrows) began 4 ms before take-off and continued once the insect was airborne with a trajectory that was upwards and slightly backwards. The wings did not open or flap in this sequence.

ridges that fluoresce bright blue under ultraviolet light. The fluorescence has the properties of the elastic protein resilin (Andersen and Weis-Fogh, 1964; Weis-Fogh, 1960) that has often been linked with cuticular devices that store energy. In lacewings, resilin is clearly located in a region that will be placed under strain when the trochanteral depressor muscle contracts, so its role may be to provide greater flexibility to the cuticle under strain and to return the thoracic structure to its natural shape after powerful muscle contractions.

Jumping mechanisms

How does the jumping mechanism of lacewings and their performance compare with those of other insects? From a survey of

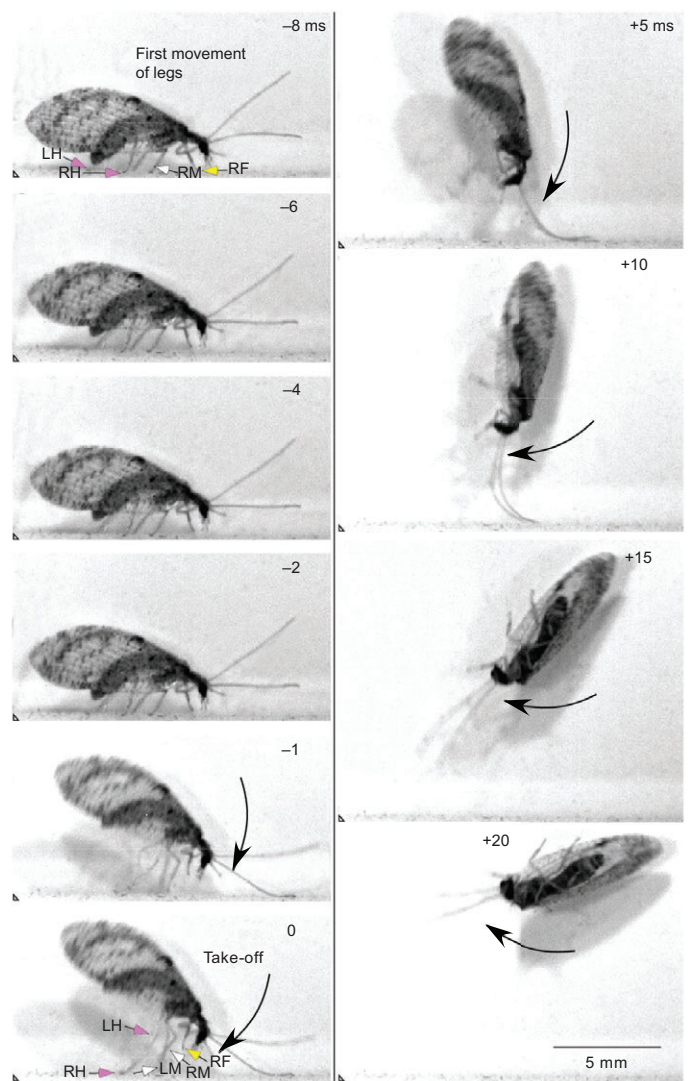


Fig. 7. Jump by a brown lacewing *Hemerobius humulinus* in which the body rotated. A downward pitch of the head (direction indicated by black arrows) occurred just before take-off as the hind legs were reaching full depression and extension. The rotation of the whole lacewing continued so that the antennae were pressed against the ground 5 ms after the legs lost contact with the ground. The wings did not open or flap during this sequence.

the jumping mechanisms that have so far been revealed in insects, the following conclusions can be drawn (Table 3).

First, the fastest take-off speeds and greatest distances and heights relative to body length achieved in a jump are generated by insects that use a catapult mechanism. Such mechanisms provide power amplification to meet the huge requirements demanded of a rapid and strong jump. The power-producing muscles contract slowly, the energy they generate is stored in distortions of specialised regions of the skeleton and then released suddenly to propel the rapid movements of the legs. Based on the orientation of the propulsive legs and the muscles used to power their movements, two broad categories of insects can be recognised. In insects such as fleas (Bennet-Clark and Lucey, 1967), flea beetles (Brackenbury and Wang, 1995) and grasshoppers (Brown, 1967), the propulsion is provided by legs arranged at the sides of the body. For example, in locusts, the energy generated by large extensor tibiae muscles is stored in cuticular distortions of the hind legs (Bennet-Clark, 1975; Burrows and Sutton, 2012). By contrast, in hemipteran bugs, the jump is propelled by short

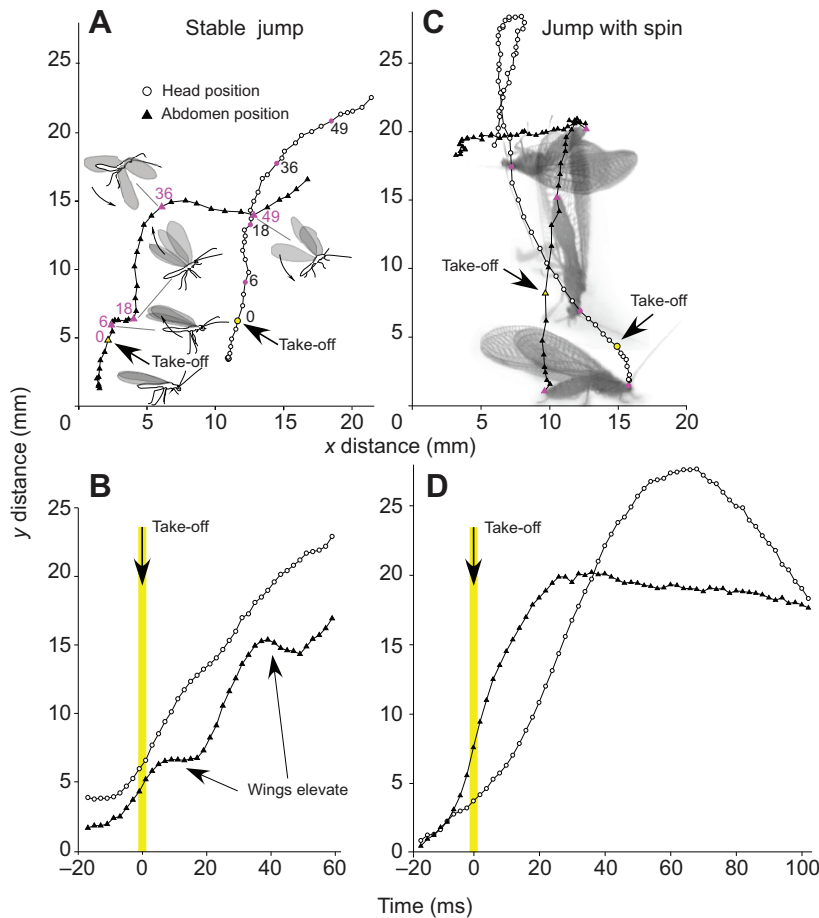


Fig. 8. Trajectories of jumps. (A,B) Jump by a green lacewing in which the body remained stable as the legs propelled take-off. The wings opened and flapped only after take-off. Note the plateaux in abdominal positions that correspond to wing elevation. (C,D) Jump by a green lacewing in which the head pitched downwards and the whole body rotated in the pitch plane, but the wings did not open or flap. (A,C) The changing x and y coordinates of the head (open circles) and tip of the abdomen (filled triangles) are plotted every 2 ms. In the bottom two graphs (B,D) the y coordinates are plotted against time every 2 ms. The cartoons in A show the position of the wings at particular times (corresponding numbers and pink symbols). The curved black arrows show the direction of wing movements. In C, three images from the video of this jump are superimposed on the corresponding points (shown in pink) on the graphs. Take-off time (0 ms) is indicated by black arrows and yellow-filled symbols in A,C and by vertical yellow bars in B,D.

legs, and thus with acceleration times of less than 1 ms, that are arranged underneath the body and the energy generated by trochanteral depressor muscles is stored in the metathoracic pleural arches (Burrows et al., 2008). In all of these insects a pre-requisite for jumping is that the legs must start from a particular position; in locusts the hind tibiae must be fully flexed about the femora (Heitler and Burrows, 1977) and in froghoppers the hind trochantera must be fully levated about the coxae (Burrows, 2006a; Burrows, 2006b).

Second, when using direct muscle contractions to power a jump, high take-off velocities can be achieved only if the propulsive legs are exceptionally long, as in bush crickets (Table 3). Even with hind legs that are 4.6 times longer than the front legs and 1.5 times longer than the body, bush crickets still cannot match the take-off velocities of similarly shaped grasshoppers that use a catapult mechanism

(Burrows and Morris, 2003). These considerable achievements also come at the expense of the much longer time it takes to move the long propulsive legs, so that acceleration times for bush crickets are longer than those of grasshoppers and more than 30 times longer than those of froghoppers. Other insects that use direct muscle contractions to power jumping, such as flies, stick insects and some ants achieve more modest take-off velocities of generally less than 1 m s^{-1} (Table 3).

Third, the lacewings analysed here, move the middle and hind pairs of legs together to propel jumping. The snow flea (*Boreus hyemalis*) (Burrows, 2011), a fly (*Hydrophorus albofloreus*) (Burrows, 2013a) and an ant (*Myrmecia nigrocincta*) (Tautz et al., 1994) also use two pairs of legs. Of these, only the snow flea apparently uses both a catapult mechanism and four propulsive legs

Table 2. Jumping performance of lacewings

	Body mass (m)	Acc. time (t)	Take-off velocity (v)	Take-off angle (Θ)	Acc. (f)	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	ms	m s^{-1}	deg	m s^{-2}	g	μJ	mW	mN	W kg^{-1}
<i>Chrysoperla carnea</i>										
Mean (N=8)	9.0±1.1 ^a	15.2±0.9	0.6±0.04	94±10	39	4.0	1.6	0.1	0.4	117
Best	10.7	19	1.0	137	54	5.5	5.6	0.3	0.6	274
<i>Micromus variegatus</i>										
Mean (N=9)	3.6±0.4 ^a	9.3±0.2	0.5±0.01	95±7	55	5.6	0.5	0.1	0.2	140
Best	3.5	10	0.6	120	62	6.3	0.7	0.1	0.2	192

The jumping performance of the lacewings analysed. Data in the four columns on the left are the grand means for the performance of three jumps by each of (N) individuals of each species; the best performance (defined by take-off velocity) of a particular individual is also given. The calculated values in the six columns on the right are derived from these measured data. Acc., acceleration.

^aN=7 for this category.

Table 3. Lacewing jumping mechanisms and performance in the context of other jumping insects

Animal	Propulsive legs	Body mass (mg)	Hind leg length		Acceleration time (ms)	Take-off velocity (m s ⁻¹)
			% of body length	% of front leg length		
Catapult mechanism						
Flea (<i>Archaeopsyllus erinacei</i>) ¹	Hind	0.7	154	190	1.2	1.9
Froghopper (<i>Philaenus spumarius</i>) ²	Hind	12.3	66	150	0.8	4.7
Leafhopper (<i>Aphrodes makarovi</i>) ³	Hind	18.4	84	220	4.4	2.9
Planthopper (<i>Issus coleoptratus</i>), male ⁴	Hind	21.5	65	120	0.8	5.5
Treehopper (<i>Entylia carinata</i>), female ⁵	Hind	5.9	86	160	1.2	2.1
<i>Hackeriella veitchi</i> (Coleorrhyncha) ⁶	Hind	1.3	65	110	1.5	1.5
Shore bug (<i>Saldula saltatoria</i>) ⁷	Hind	2.1	90	180	4	1.8
Jumping plant lice (<i>Psylla alni</i>), female ⁸	Hind	2.8	61	120	1.7	2.7
Snow flea (<i>Boreus hyemalis</i>), female ⁹	Middle	4.2	130	140	6.6	0.9
	Hind		170	187		
Locust (<i>Schistocerca gregaria</i>), female ¹⁰	Hind	2000	100	320	20	3.2
<i>Prosartharia teretirostris</i> , male ¹¹	Hind	1540	62	260	30	2.5
Direct muscle contraction						
Green lacewing (<i>Chrysoperla carnea</i>)	Middle	9	38	120	15	1
	Hind		55	170		
Brown lacewing (<i>Micromus variegatus</i>)	Middle	3.6	35	150	9	0.6
	Hind		70	210		
Bush cricket (<i>Pholidoptera griseoptera</i>), female ¹²	Hind	600	158	460	32.6	2.1
Bush cricket, male ¹²	Hind	415	152	420	30.6	1.5
Fly (<i>Hydrophorus alboflorens</i>) ¹³	Middle	4.7	170	140	21.1	1.6
	Hind		170	140		
Ant (<i>Myrmecia nigrocincta</i>) ¹⁴	Middle and hind	–	–	–	15–25	0.6–0.7
Stick insect (<i>Sipyloidea</i> sp.), male ¹⁵	Hind	164	64	100	100	0.6
Stick insect (<i>Timema chumash</i>) ¹⁶	Hind	47.5	57	150	12	0.9

The insects listed are divided into two groups; those which have jumps involving a catapult mechanism, and those with jumps powered by direct muscle contractions. Mean data values are taken from this paper and from papers listed below. Take-off velocities are the highest recorded for each species.

¹(Sutton and Burrows, 2011); ²(Burrows, 2006a); ³(Burrows, 2007a); ⁴(Burrows, 2009a); ⁵(Burrows, 2013b); ⁶(Burrows et al., 2007); ⁷(Burrows, 2009b);

⁸(Burrows, 2012); ⁹(Burrows, 2011); ¹⁰(Bennet-Clark, 1975); ¹¹(Burrows and Wolf, 2002); ¹²(Burrows and Morris, 2003); ¹³(Burrows, 2013a); ¹⁴(Tautz et al., 1994); ¹⁵(Burrows and Morris, 2002); ¹⁶(Burrows, 2008).

(Burrows, 2011). How all four legs are moved to deliver their power at the same time remains to be explained.

Why does this third group of insects use four propulsive legs? Two reasons can be advanced. First, the ground reaction forces will be distributed over a larger area provided by the four tarsi and over a longer time because acceleration times are slower, compared with insects of a similar mass using a catapult mechanism. This enables lacewings to jump from flexible leaves, snow fleas to jump from snow (Burrows, 2011) and the fly *H. alboflorens* to jump from the surface of water (Burrows, 2013a). Second, snow fleas, *H. alboflorens* and lacewings all have thin legs so that using two pairs, and thereby doubling the muscle mass used for jumping, may be the only way of generating enough power to launch into the air. Snow fleas are wingless and must rely only on the legs for propulsion. By contrast, *H. alboflorens* moves its wings at the same time as it moves its legs and in some take-offs makes only small movements of the legs. Nevertheless, the jumps powered by both legs and wings have a take-off velocity that is 168% faster and an acceleration time that is 84% shorter than take-off powered only by the wings. Lacewings do not move the wings until they are airborne, so they use only the middle and hind legs to generate take-off.

Two jumping strategies

In jumps by both green and brown lacewings, two different jumping strategies were recognised. In the first and most commonly observed strategy (59% of jumps in green lacewings, 65% in brown lacewings) the body remained stable during take-off and did not spin after take-off when the wings began to open several milliseconds into the airborne phase. The propulsive movements of the legs therefore

launched the lacewing into the air and led smoothly to flapping flight. In the second strategy (41% of jumps in green lacewings, 35% in brown lacewings), the body spun in the pitch plane once airborne at rates of up to 22 Hz and in only one of the jumps by each type of lacewing did the wings open. The most obvious difference between the two categories was the angle of the body relative to the horizontal at take-off. In the first strategy, the body was close to parallel with the ground or pointed just above or below it (green lacewings, -7 ± 8 deg; brown lacewings, 13.7 ± 7 deg). In the second strategy, the head always pointed downwards so that the body subtended an angle of -37 ± 3 deg (green lacewings) and -35 ± 4 deg (brown lacewings). For both green and brown lacewings the body angles for the two jumping strategies were significantly different (see Results); each adopted different body angles when they jumped with spin and without spin. There was, however, no significant difference in the body angle at take-off adopted by either a green or a brown lacewing when jumping without spin. Similarly, there was no significant difference in the body angle used by the two types of lacewing when jumping with spin. We conclude that the two types of lacewings both use the same strategy to generate jumps that are either stable (no spin) or unstable (with spin). The leg movements were apparently the same in the two jumping strategies so that the different angle of the body, and presumably the resulting position of the centre of mass, relative to where the thrust is applied must determine the amount of spin. This was reflected in different jumps in which there was a strong correlation between body angle and spin rate. A further difference was that jumps in the first category (no spin but flapping wing movements after take-off) took longer to reach a particular height than those in the second category in which the body spun but the wings did not flap.

For example, to reach a height of 22 mm it took 58 ms using the first strategy but only 42 ms using the second, a 38% decrease between the two types of jump (Fig. 8). The gain in height was clearly slowed at each elevation of the wings.

Avoiding spin, and hence the loss of energy to rotation instead of translating it to forward movement, would seem to be advantageous for many jumping insects, but the ability to adjust the centre of mass relative to the point where force is applied can lead to other advantages. Jumping insects with the highest spin rates (480 Hz in the pitch plane) are springtails (*Collembola*) (Christian, 1979). They propel themselves by extending a furca at the end of their abdomen. This point of force application is distant from the centre of the mass and seemingly leaves little scope for adjustment and thus avoiding spin. In most jumps by Psyllids (jumping plant lice: Hemiptera, Sternorrhyncha, Psyllidae) the head again points downwards at take-off, so that the propulsive movements of the hind legs, which are arranged at the sides of the thorax, as in lacewings, impart a forward rotation to the body and spin rates in the pitch plane as high as 336 Hz (Burrows, 2012), or 15 times higher than in lacewings. Nevertheless, Psyllids also have a second jumping strategy, that although much less common (2% of its jumps), results from the same adjustment of the body angle at take-off as in lacewings. If the head points upwards at take-off then the spin rate is reduced. Pygmy mole crickets, spin backwards at rates above 100 Hz, which is suggested to be a mechanism for adding unpredictability to the jumps given that their neighbours are dangerous predators (Burrows and Picker, 2010). In flea beetles the forward spin rates range from 21 to 187 Hz in different species (Brackenbury and Wang, 1995) and in planthoppers are between 40 and 90 Hz (Burrows, 2009a).

What evolutionary advantage could spinning add to jumping? First, it will add to the unpredictability of the trajectory of a jump and the subsequent site for landing and thus make it harder for a predator to catch an insect. Second, if the spin rate can be varied, then the task of a predator will be made even harder. Such survival advantages as these must outweigh those where all the energy is put into achieving the highest velocity of a jump and argue that jumping is both a mechanism of escape from predators and a fast and efficient way of moving from one place to another amongst vegetation.

Biology of the jump

To allow ready comparison with the jumping performance of other insects, only the jumps from a horizontal surface were considered in these analyses of lacewings. In their natural habitat, however, lacewings jump readily from leaves and stems with many different orientations, frequently emerging from hiding places on the undersides of leaves. It is, however, not known what natural stimuli elicit jumps and whether some lead to stable jumps and others to tumbling jumps. In flies, for example, different stimuli clearly lead to different types of jumping behaviour (Card, 2012). In lacewings, jumps from an upright posture, or in response to certain stimuli in which the body remains stable may generate a directed movement to a particular target. In other orientations, an unstable jump with a tumbling motion adds further unpredictability that may improve survival chances in the presence of a predator.

MATERIALS AND METHODS

Green lacewings of the *Chrysoperla carnea* group, (see Henry, 1985; Henry et al., 2001; Tauber and Tauber, 1973) and brown lacewings *Micromus variegatus* (Fabricius, 1793) were caught in Girton, Cambridge, UK in August and September 2013. No attempt was made to identify individual green lacewings to the level of sibling species, for example, according to their song patterns (Henry et al., 2002). A few specimens of the brown

lacewing *Hemerobius humulinus* Linnaeus 1761, also caught in the same place, were filmed but their morphometrics were not analysed in detail. All these lacewings belong to the order Neuroptera, the green lacewings to the family Chrysopidae and the brown ones to the family Hemerobiidae.

The anatomy of the hind legs and metathorax was analysed in 10 green lacewings and nine brown lacewings. Intact lacewings were photographed and drawn and those preserved by fixation in: 5% buffered formaldehyde and subsequent storage in 70% alcohol; fixation and storage in 70% alcohol, or in 50% glycerol, were also analysed. Colour photographs were taken with a Nikon DXM1200 digital camera attached to a Leica MZ16 stereo microscope (Wetzlar, Germany). Lengths of the legs of fixed specimens were measured to an accuracy of 0.1 mm with a ruler placed on images projected onto a large screen from the same microscope. Body masses were determined to an accuracy of 0.1 mg with a Mettler Toledo AB104 balance (Beaumont Leys, Leicester, UK). To make statistical tests on both the morphological and kinematical experiments, data were determined to be normally distributed by using the Shapiro–Wilk test and then parametric *t*-tests were applied assuming equal variance.

To search for the possible presence of the rubber-like protein resilin, lacewings were viewed through Olympus MPlan 5×/0.1 NA and 10×/0.25 NA objective lenses, under UV or white epi-illumination on an Olympus BX51WI compound microscope (Olympus UK, London, UK). UV light from an X-cite series 120 metal halide light source (EXFO, Chandlers Ford, UK) was conditioned by a Semrock DAPI-5060B Brightline series UV filter set (Semrock, Rochester, NY, USA) with a sharp-edged (1% transmission limits) band from 350 nm to 407 nm. The resulting blue fluorescence emission was collected at wavelengths from 413 nm to 483 nm through a similarly sharp-edged bandpass filter and dichroic beam splitter. UV and brightfield images of the same regions of the thorax were superimposed with Canvas 14 (ACD Systems International Inc., Seattle, WA, USA).

Sequential images of jumps were captured at rates of 1000 s⁻¹ and an exposure time of 0.5 ms with a single Photron Fastcam SA3 camera (Photron (Europe) Ltd, West Wycombe, Bucks., UK). The images, with a resolution of 1024×1024 pixels, were fed directly to a computer for later analysis. Jumps occurred spontaneously, or were elicited by delicate mechanical stimulation with a 100 μm silver wire, in a chamber made of optical quality glass (width, 55 mm; height, 55 mm; depth, 27 mm). The floor, sides and ceiling from which the lacewings could jump, were made of high density foam (Plastazote, Watkins and Doncaster, Cranbrook, Kent, UK). The camera, fitted with a 100 mm micro Tokina lens, or a 60 mm Micro Nikkor lens, pointed at the middle of this chamber, the shape of which constrained most jumps to the image plane of the camera. Measurements of distances moved were made from jumps that were parallel to the image plane of the camera, or as close as possible to this plane. Jumps that deviated from the image plane of the camera by more than 30 deg were not included in the analysis. Those that deviated by up to 30 deg were calculated to result in a maximum error of 10% in the measurements. Changes in joint angles were measured from these images and from those captured from underneath as a lacewing jumped from the vertical front of the chamber. Selected image files were analysed with Motionscope camera software (Redlake Imaging, Tucson, AZ, USA) or with Canvas 14. Take-off time, designated as *t*=0 ms, was defined as the time at which the all legs lost contact with the ground and the lacewing became airborne and thus allowed different jumps to be compared. The acceleration time of a jump was defined as the period from the first detectable, propulsive movement of the legs until take-off. A one-frame error in estimating both the first movement of the legs and 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 three point average of measurements taken from successive images, and the values presented are for the final millisecond before take-off. Fifty-five jumps by eight green lacewings and 60 jumps by nine brown lacewings were recorded. A minimum of five jumps were recorded for each lacewing. Only jumps from the floor of the chamber were analysed in detail. Measurements are given as means ± s.e.m. Temperatures in all experiments ranged from 22 to 25°C.

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Author contributions

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Supplementary material

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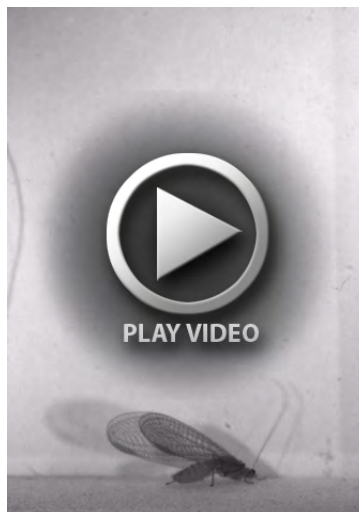
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Movie 1. Side view of the green lacewing *Chrysoperla carnea* group, captured at 1000 frames s^{-1} and replayed at 10 frames s^{-1} , as it jumped from the floor of the experimental chamber. The body did not spin and wing movements in flapping flight did not begin until the insect became airborne. See also Fig. 3.



Movie 2. Side view of the brown lacewing *Micromus variegatus* captured at 1000 frames s^{-1} and replayed at 10 frames s^{-1} , as it jumped from the floor of the experimental chamber. See also Fig. 4.



Movie 3. A side view of the green lacewing *Chrysoperla carnea* group captured at 1000 frames s^{-1} and replayed at 10 frames s^{-1} , as it jumped from the floor of the experimental chamber. The head pointed downwards during the acceleration phase of the jump and once airborne the body spun in the pitch plane. The wings did not open or generate flapping flight once airborne. See also Fig. 6.