

RESEARCH ARTICLE

Jumping mechanisms in jumping plant lice (Hemiptera, Sternorrhyncha, Psyllidae)

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SUMMARY

Jumping mechanisms and performance were analysed in three species of psyllids (Hemiptera, Sternorrhyncha) that ranged from 2 to 4 mm in body length and from 0.7 to 2.8 mg in mass. Jumping was propelled by rapid movements of the short hind legs, which were only 10–20% longer than the other legs and 61–77% of body length. Power was provided by large thoracic muscles that depressed the trochantera so that the two hind legs moved in parallel planes on either side of the body. These movements accelerated the body to take-off in 0.9 ms in the smallest psyllid and 1.7 ms in the largest, but in all species imparted a rapid forward rotation so that at take-off the head pointed downwards, subtending angles of approximately -60° relative to the ground. The front legs thus supported the body just before take-off and either lost contact with the ground at the same time as, or even after, the hind legs. In the best jumps from the horizontal, take-off velocity reached 2.7 ms^{-1} and the trajectory was steep at $62\text{--}80^\circ$. Once airborne, the body spun rapidly at rates of up to 336 Hz in the pitch plane. In many jumps, the wings did not open to provide stabilisation, but some jumps led directly to sustained flight. In their best jumps, the smallest species experienced a force of 637 g. The largest species had an energy requirement of $13 \mu\text{J}$, a power output of 13 mW and exerted a force of nearly 10 mN. In a rare jumping strategy seen in only two of 211 jumps analysed, the femoro-tibial joints extended further and resulted in the head pointing upwards at take-off and the spin rate being greatly reduced.

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INTRODUCTION

Jumping as a fast means of locomotion or escape is widespread amongst the four sub-orders of hemipteran insects, most of which move their hind legs in the same plane beneath the body, while others, including the subjects of this paper, the psyllids, move them along the sides of the body. Jumping performance reaches its peak in the Auchenorrhyncha; the frog hopper (spittle bug) *Philaenus spumarius* and the planthopper *Issus coleoptratus* have the best jumping performance of any insect described so far. They accelerate their bodies in less than 1 ms to a take-off velocity of 4.7 and 5.5 ms^{-1} , experiencing a force of 550 and 720 g, respectively (Burrows, 2003; Burrows, 2006; Burrows, 2009a). This exceptional performance is accomplished by a catapult mechanism. Large forces are developed by the slow contraction of enormous thoracic muscles that store energy by bending paired bow-shaped elements of the internal skeleton. These energy stores are built of a composite of hard cuticle and the soft elastic protein resilin (Burrows et al., 2008). Sudden release of the stored energy then powers the rapid and simultaneous depression of the hind legs (Burrows, 2007b).

In a second hemipteran sub-order, the basal Coleorrhyncha, at least one wingless species jumps, but it shows few specialisations for jumping (Burrows et al., 2007). Its hind legs are only 10% longer than the other legs and their rapid movements accelerate it in 1.5 ms to a take-off velocity of 1.5 ms^{-1} . This insect experiences a force of 100 g and, once airborne, rotates about any of the three body axes.

A third sub-order, the Heteroptera, contains a wide diversity of bugs, but only two families have species that are reported to jump,

and only one of these, the Saldidae or shore bugs, has been investigated in detail (Burrows, 2009b). The hind legs of these bugs are 80% longer than the other legs and in 25% of all jumps are used as the sole means of accelerating the body in 4 ms to a take-off velocity of 1.2 ms^{-1} . The majority of its jumps are, however, accompanied by movements of the wings and achieve similar take-off velocities and similar jumping performance.

Jumping abilities of members of a fourth sub-order, the Sternorrhyncha, which includes aphids, coccids and whiteflies, have not been analysed, although one group, the Psylloidea or jumping plant lice, are, as their colloquial name implies, renowned for their jumping. The group is widespread throughout many parts of the world although individual species generally feed on the phloem of a particular species of usually dicotyledonous plants. On many crop species as diverse as carrot, olive, pear and apple, they can become a pest, but can also be beneficial in controlling some alien invasive plants such as broom and mesquite. The anatomy of the thorax and hind legs of this group has been well described (Crawford, 1914; Weber, 1929). The present paper shows that jumps by three species of psyllids are propelled by the hind legs, under the control of large trochanteral muscles in the thorax. The jumps are characterised by an unusual take-off posture in which the head points downwards and the front tarsi provide support for the body in a movement that resembles a human handstand. Once airborne, the body spins at high rates in the pitch plane. Energy is thus lost to rotation but the body is nevertheless accelerated rapidly to a take-off velocity of 2.7 ms^{-1} . A rarely used strategy involving more extensive movements of

the femoro-tibial joints of the hind legs enables take-off with the head up and with a greatly reduced rate of body spin.

MATERIALS AND METHODS

Three species of psyllids were caught on their host trees in Girtton, Cambridge, UK, in Ljubljana, Slovenia and in Aachen, Germany: (1) *Cacopsylla peregrina* (Foerster), from hawthorn (*Crataegus monogyna*); (2) *Psyllopsis fraxini* (L.), from ash (*Fraxinus excelsior*); (3) *Psylla alni* (L.), from alder (*Alnus glutinosa*). They all belong to the order Hemiptera, the sub-order Sternorrhyncha and the family Psyllidae.

Sequential images of jumps were captured at 5000 frames s^{-1} and with an exposure time of 0.05 ms with a single Photron Fastcam 1024PCI high-speed camera [Photron (Europe) Ltd, West Wycombe, Buckinghamshire, UK], fitted with a 60 mm Nikon lens. The images were fed directly to a laptop computer. The jumps either occurred spontaneously or after the psyllids had been manoeuvred with a fine paint brush toward the middle of a glass chamber, which measured 80 mm wide, 40 mm tall and 10 mm deep at floor level, widening to 25 mm at the top. The floor was of high-density foam. Some jumps were also captured from vertically placed pieces of the same foam. The camera pointed at the centre of this chamber. A psyllid was able to jump in any direction. Detailed measurements of changes in joint angles and 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 to either side of the image plane of the camera by up to $\pm 30^\circ$ would result in a maximum error of 10% in the measurements of leg joint, or body angles. Sequences of images 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 legs lost contact with the ground and the psyllid became airborne was designated as $t=0$ ms, thus allowing different jumps by the same or different psyllids to be compared. The time at which the 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. Peak velocity was calculated as the distance moved in a rolling three-point average of successive frames captured at 0.2 ms intervals before take-off. The measured point on the body was close to the centre of mass, just behind the hind legs. Movies 1 and 2 in the supplementary material show characteristic jumps.

The anatomy of the hind legs and metathorax was examined in intact psyllids and in those preserved in either 70% alcohol or 50% glycerol. Drawings of the legs, joints and muscles were made with the aid of a drawing tube attached to a Leica MZ16 stereo microscope (Wetzlar, Germany). Individual colour photographs were taken with a Nikon DXM1200 digital camera attached to the same microscope.

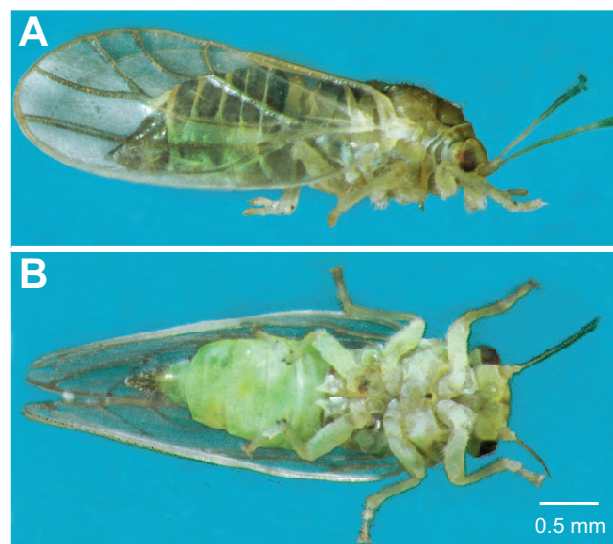


Fig. 1. Photographs of *Psylla alni*. (A) Side view. (B) Ventral view.

Dried specimens were also mounted on specimen holders, sputter-coated with gold and then examined in a Philips XL-30 scanning electron microscope (Philips, Eindhoven, The Netherlands). Lengths of the parts 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 and projected onto a 24" monitor. Body masses were determined to an accuracy of 0.1 mg with a Mettler Toledo AB104 balance (Beaumont Leys, Leicester, UK).

A total of 211 jumps by 41 psyllids were captured and analysed; 113 jumps by 17 hawthorn psyllids (*Cacopsylla*), 32 jumps by five ash psyllids (*Psyllopsis*) and 66 jumps by 19 alder psyllids (*Psylla*). Measurements of body mass were made on these psyllids and on other members of the same species whose jumps were not recorded. Measurements are given as means \pm standard error of the mean (s.e.m.). Temperatures in all experiments ranged from 23 to 26°C.

RESULTS

Body shape

All three species of psyllids analysed had a similar body shape, with large translucent front wings held to form a roof covering the thorax and abdomen and extending beyond the tip of the abdomen (Fig. 1A,B). The body was slung low to the ground and supported by legs placed on the ground to either side of the body. *Cacopsylla* was the smallest, with a body length of 1.9 ± 0.1 mm (mean \pm s.e.m., $N=13$) and a body mass of 0.7 ± 0.03 mg ($N=35$). *Psylla* was the largest, with a body twice the length of the other two species (4.0 ± 0.3 mm; $N=7$) and of almost four times greater mass (2.8 ± 0.1 mg; $N=29$) than *Cacopsylla* (Table 1). *Psyllopsis* had a body

Table 1. Body form in psyllids

Insect	Body length (mm)	Body mass (mg)	Hind leg tibia (mm)	Hind leg femur (mm)	Ratio of leg lengths (front: middle: hind)	Hind leg length (% of body length)	Hind leg length (mm) / cube root of body mass (mg)
<i>Cacopsylla peregrina</i> (hawthorn psyllid)	1.9 ± 0.1 (13)	0.7 ± 0.03 (35)	0.5 ± 0.02 (13)	0.5 ± 0.02 (13)	1:1:1.1	66	1.5
<i>Psyllopsis fraxini</i> (ash psyllid)	2.2 ± 0.1 (7)	1.2 ± 0.1 (19)	0.9 ± 0.02 (7)	0.6 ± 0.01 (7)	1:1:1.2	76	1.6
<i>Psylla alni</i> (alder psyllid)	4.0 ± 0.3 (7)	2.8 ± 0.1 (29)	1.0 ± 0.1 (7)	0.8 ± 0.02 (7)	1:1:1.2	61	1.7

Body length and mass, and lengths of the hind femora and tibiae, in three species of psyllids are given as means \pm s.e.m.; the number of individuals from which the measurements were taken is given in parentheses. The ratio of leg lengths is given relative to the front legs.

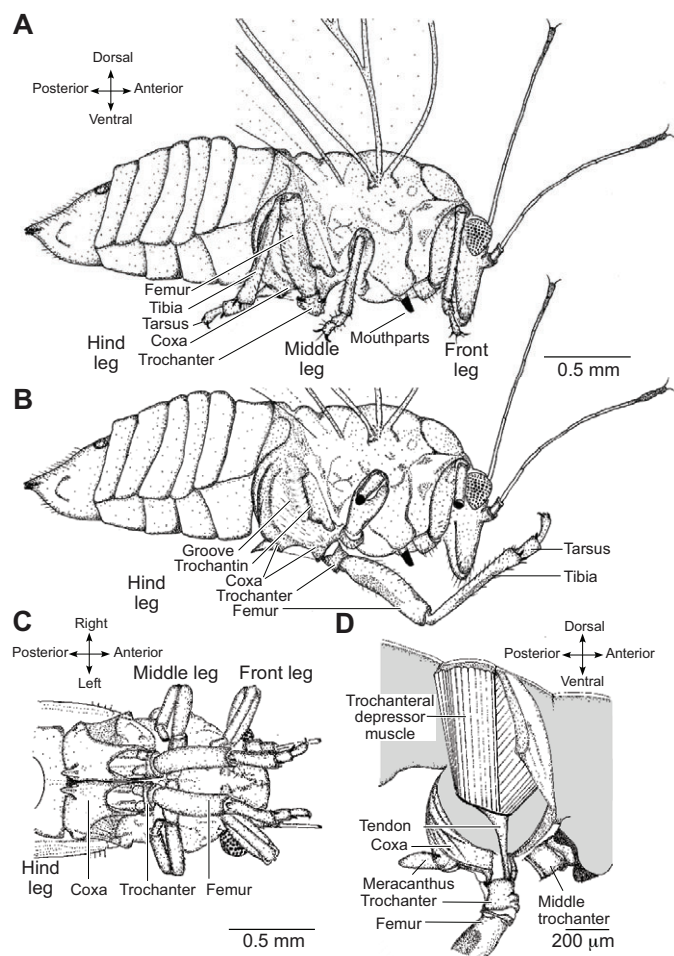


Fig. 2. Drawings of *Psyllopsis fraxini*. (A) View of the right side, with the right hind leg fully levated and ready to propel a jump. The femur locates in a hollowed and membranous area of the side wall of the metathorax bounded anteriorly by the trochantin. (B) The same view, with the right hind leg fully depressed, as it would be at the end of a jump. The large coxa of the right hind leg is now visible. The tibiae and tarsi of the front and middle legs are omitted. (C) Ventral view, with the hind legs fully depressed and pointing forwards. (D) The left half of the metathorax, viewed from inside, to show the large trochanteral depressor muscle of a hind leg and its tendon.

only 10% longer than that of *Cacopsylla* (2.2 ± 0.1 mm; $N=7$) but a body mass that was 62% greater (1.2 ± 0.1 mg; $N=19$).

Structure of the hind legs

In *Cacopsylla*, the hind legs were only 10% longer than the front and middle legs, giving a ratio of leg lengths of 1:1:1.1 front:middle:hind (Table 1). In *Psylla* and *Psyllopsis*, the hind legs were 20% longer than the front and middle legs, giving a ratio of leg lengths of 1:1:1.2. In *Cacopsylla*, the hind tibia was the same length as the hind femur, but in *Psylla* it was 25% longer and in *Psyllopsis* it was 50% longer. Relative to the length of the body, the hind legs were also short, ranging from 61% of body length in *Psylla*, to 66% in *Cacopsylla* and to 76% in *Psyllopsis*. Relative to the cube root of body mass, the ratio of the hind leg lengths had a similar ratio, ranging from 1.5 to 1.7.

The two large hind coxae were closely apposed at the midline and did not move visibly relative to the metathorax during jumping

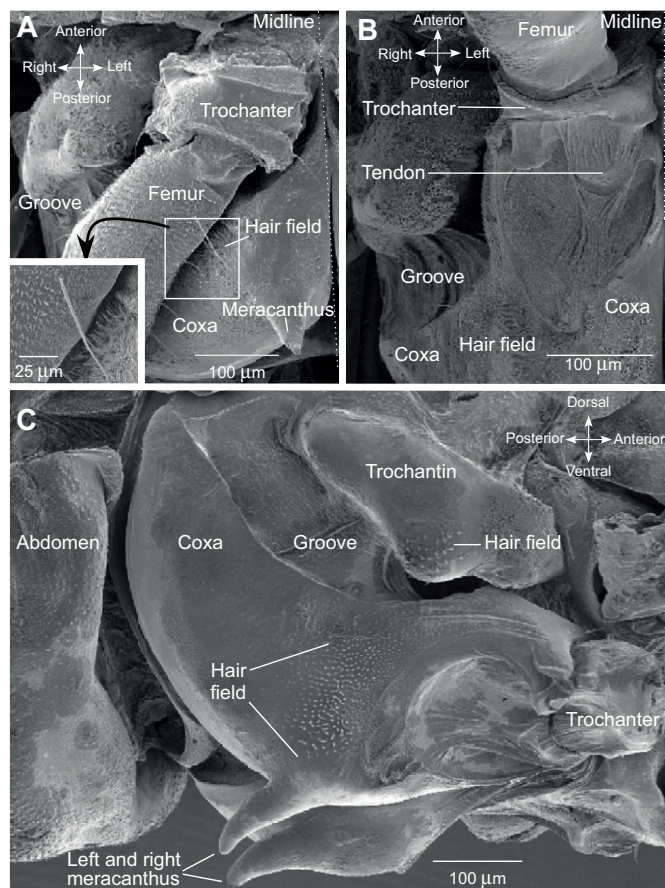


Fig. 3. Scanning electron micrographs of the right hind leg of *Psylla alni*. (A) Ventral view of the right trochanter and femur, which lies in a groove in the side wall of the thorax, bounded anteriorly by the trochantin. A pointed meracanthus projects posteriorly from the coxa. The inset shows the dorsal surface of the femur touching the edge of a hair field on the coxa. (B) Ventral view of the right hind trochanter, which is fully depressed so that the hind leg points anteriorly and reveals the articulation of the trochanter with the coxa. The insertion of the tendon of the large trochanteral depressor muscle is visible. (C) Lateral view of the right hind leg of *Psylla alni*. The hind leg is depressed fully so that it projects forwards to reveal the articulation between the right trochanter and the coxa and the groove between the coxa and trochantin. Two hair fields are visible; the larger with more densely packed sensilla on the coxa, and a smaller one on the trochantin.

(Figs 2, 3). By contrast, the small trochanter rotated through some 220 deg about the coxa and swung the hind leg from its fully levated position before a jump (Fig. 2A) to its fully depressed position after take-off (Fig. 2B, C, Fig. 3B). In its fully levated position, the hind femur fitted into a groove in the coxa at the side of the body and abutted anteriorly with the trochantin (Fig. 1A, Fig. 3). At its fully depressed position, the hind tibia and tarsus projected anteriorly in front of the head. A pointed protrusion, the meracanthus (Fig. 2A, B, D, Fig. 3) projected posteriorly and ventrally from the coxa but did not appear to engage with any part of the hind leg during these movements. The femur rotated through a small angle about the trochanter; the tibia through some 110 deg about the femur, and the tarsus through some 70 deg about the tibia. Ventrally pointing spines were present on the distal tibia at the tibio-tarsal joint, which could increase traction with the surface from which a psyllid jumps.

Depression of the trochanter was powered by large muscles located in the metathorax (Fig. 2D). The muscles arise from the

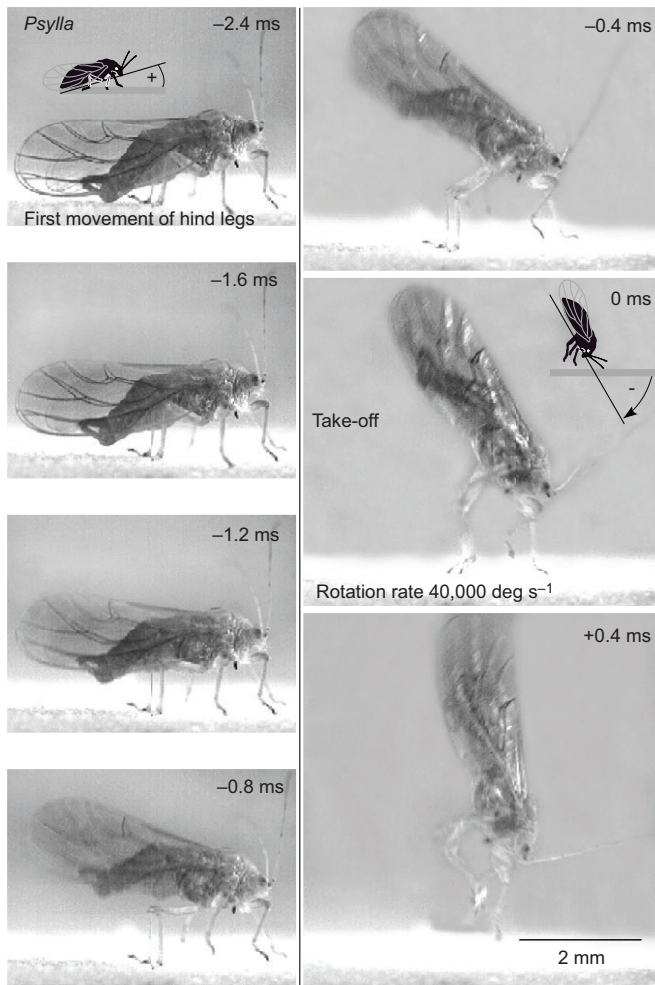


Fig. 4. Images of a jump by *Psylla alni*, viewed from the side and captured at 5000 s^{-1} , each with an exposure time of 0.05 ms. The images are arranged in two columns, with the bottom left-hand corner of each image providing a constant reference point in this and in Figs 5, 7–9. The hind legs started to move at -2.4 ms , and the continuing depression of the hind trochanter raised the rear of the body so that the middle legs lost contact with the ground and the head pitched forwards. Once airborne, the body rotated rapidly in the pitch plane. The cartoons show how the angle of the body relative to the ground was measured when the head was pointing upwards (frame -2.4 ms) and then downwards (frame 0 ms).

dorsal and anterior walls of the metathorax and insert within the thorax on a large, stiff tendon that runs through the coxa to insert on the medial, ventral rim of the trochanter (Fig. 2D).

A number of hair fields are placed such that they could provide proprioceptive information about the movement or position of a hind leg (Fig. 3). On the ventral surface of the hind coxae were two symmetrically placed fields that would be contacted by a hind femur when it was levated (Fig. 3A). Each field consisted of numerous articulated hairs, $25\text{--}50\text{ }\mu\text{m}$ in length and thus much shorter than the sparse $500\text{ }\mu\text{m}$ trichoid sensillum located nearby on the femur (inset in Fig. 3A). These fields were exposed when the hind legs were depressed (Fig. 3B), revealing the gradation in length of their constituent hairs. When levated, a hind leg also engaged with a hair field on the lateral surface of the coxa, which again consisted of a large number of short hairs (Fig. 3B,C). On the ventral and posterior part of the trochantin was another hair field that would be contacted

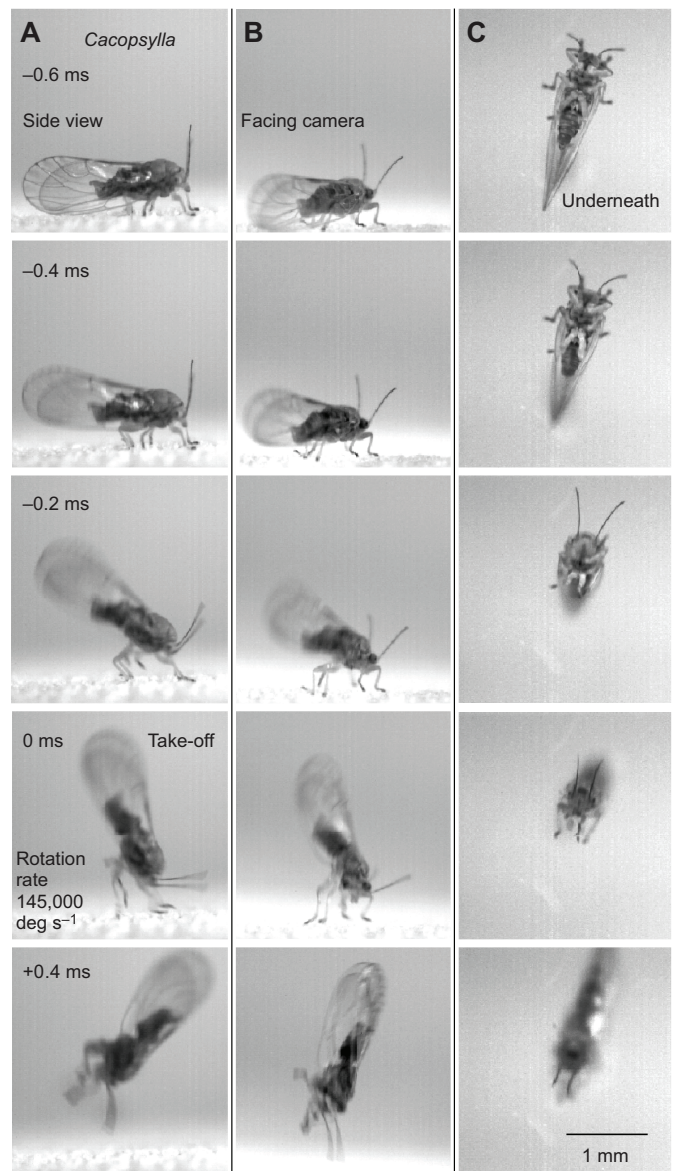


Fig. 5. Images of three jumps by the same *Cacopsylla peregrina* viewed from different orientations to show the sequence of movements of the hind legs. Images were captured at 5000 s^{-1} , each with an exposure time of 0.05 ms. (A) Jump viewed from the side. (B) Jump towards and to the right of the camera. (C) Jump from the front, glass wall of the chamber and viewed from underneath.

by the hind femur in advance of the jump (Fig. 3A,C). Together, these hair fields should be able to signal the initial levated position of a hind leg before a jump and its depressed position once a jump has been propelled.

Kinematics of the jump

The following description is of jumping by *Psylla*, the largest of the psyllids studied (Figs 4, 6), with further characteristics illustrated by the other two species (Figs 5, 7). The key feature of the jump was that the propulsive movements of the hind legs rotated the head downwards so that the front legs were often the final means of support. This posture at take-off resulted in high rates of spin in the pitch plane once airborne (Figs 4–6; supplementary material

Table 2. Jumping performance of psyllids

	Body mass (<i>m</i>)	Time to take off (<i>t</i>)	Take-off velocity (<i>v</i>)	Take-off angle	Body angle at take-off	Acceleration (<i>f</i>)	<i>g</i> force	Energy (<i>E</i>)	Power (<i>P</i>)	Force (<i>F</i>)	Rotation
Formula						$f=v/t$	$g=f/9.86$	$E=(0.5m)v^2$	$P=E/t$	$F=mf$	
Units	mg	ms	ms ⁻¹	deg	deg	ms ⁻²	<i>g</i>	μJ	mW	mN	Hz
<i>Cacopsylla peregrina</i>											
Mean	0.7±0.1	0.9±0.3	1.7±0.2	80±1	-61±5	1910	195	1.1	1.2	1.4	336±14
Maximum	1	0.4	2.5			6250	637	3.1	7.8	6.3	
<i>Psylloopsis fraxini</i>											
Mean	1.2±0.1	1.2±0.2	1.1±0.1	62±7	-58±3	910	93	0.8	0.6	1.1	199±17
Maximum	1.5	0.8	1.9			2340	240	2.6	3.3	3.5	
<i>Psylla alni</i>											
Mean	2.8±0.1	1.7±0.2	1.7±0.2	76±6	-66±3	1060	108	4.6	2.7	3.0	221±11
Maximum	3.6	1.0	2.7			2700	275	13.1	13.0	9.7	

The jumping performance of three species of psyllids. The data are the mean of means for the performance of individuals; 40 jumps by eight *Cacopsylla*, 19 jumps by five *Psylloopsis* and 32 jumps by seven *Psylla*, with a minimum of three jumps by each psyllid. The best (maximum) performance of a particular individual for each species is also given.

Movie 1). Before a jump, both hind legs were fully levated so that the anterior edge of each femur was pressed against the associated trochantin. The body was held at an angle of about +20 deg relative to the horizontal so that the tip of the abdomen was close to the ground and the head was raised by the front and middle legs (Fig. 4, see diagram on first frame). The first observable movement of a hind leg was depression of the trochanter about the coax, which resulted in the progressive downward movement of the femur (supplementary material Movie2). Initially, the angle between the femur and the tibia did not change, but as the rotation of the trochanter continued, then from 0.4 ms before take-off, the tibia did begin to extend. At take-off, the tibia was almost fully extended about the femur and the angle of the body relative to the horizontal was -76±6 deg (Table2, Fig. 4, see diagram on frame 0 ms) with the head pointing downwards. During the 2.4 ms acceleration period in this jump, the angular rotation of the body was therefore 40,000 degs⁻¹. The middle legs were the first to lose contact with the ground, between 0.6 and 0.4 ms before take-off. The forward pitch of the body was so great that the front legs supported the body until take-off. The angular movements of the joints of the front legs indicated that they were providing balance rather than thrust to the jump. Take-off was marked by the front and hind legs losing contact with the ground at about the same time. After take-off, rapid rotation of the body continued in the pitch plane.

Three jumps by the same psyllid *Cacopsylla* – viewed from the side (Fig. 5A), from in front as it jumped towards the camera (Fig. 5B) and from underneath as it jumped from the vertical glass wall of the chamber (Fig. 5C) – illustrate further features of the sequence of leg movements. Before the jump, the tarsi of the hind legs were placed lateral to the body and remained in that position as they transmitted the force generated by the trochanteral muscles in the thorax to the ground. The rotation of the trochantera resulted in the femoro-tibial joints of the two hind legs moving medially and thus closer to each other so that they came to lie underneath the body (Fig. 5C). The body was pitched forwards at even higher angular rotation rates of 145,000 degs⁻¹ during the much shorter (0.6 ms long) acceleration period. Take-off was again marked by the front and hind legs losing contact with the ground at about the same time. In all species, the body always pointed downwards at take-off with the head close to the ground and the abdomen raised in the air. Body angles at take-off were similar in all species, ranging

from -58±3 deg in *Psylloopsis* (mean of means of 19 jumps by five psyllids), to -61±5 deg in *Cacopsylla* (mean of means of 40 jumps by eight psyllids) and to -66±3 deg in *Psylla* (mean of means of 32 jumps by seven psyllids) (Table2). The numbers of jumps and animals given here also apply to subsequent data.

The time taken to accelerate to take-off was related to the body mass of a particular species of psyllid. In the lightest species, *Cacopsylla*, the acceleration time was shortest, with a mean of 0.9±0.3 ms and with a fastest acceleration of only 0.4 ms in the best jump recorded. In *Psylloopsis*, the time rose to 1.2±0.2 ms (fastest 0.8 ms) and in the heaviest species, *Psylla*, acceleration took almost twice as long as in *Cacopsylla* at 1.7±0.2 ms (fastest 1.0 ms) (Table2). By contrast, the velocity at take-off did not correlate with body mass; both the lightest and the heaviest had the same take-off velocities [*Cacopsylla* 1.7±0.2 ms⁻¹ (fastest 2.5 ms⁻¹), *Psylla* 1.7±0.2 ms⁻¹ (fastest 2.7 ms⁻¹)], with *Psylloopsis*, of intermediate mass, having the lowest take-off velocity of 1.1±0.1 ms⁻¹ (fastest 1.9 ms⁻¹) (Table2).

In the experimental chamber, psyllids jumped from the horizontal floor or from a vertical surface (Fig. 6A,B), but in their natural habitat they often jumped from the under-surface of leaves. No matter what the starting position, the thrust and spin that was imparted by movements of the hind legs translated into two characteristic features of the jump trajectory.

First, the angle of the trajectory was steep. Take-off elevation was controlled by the posture of the front and middle legs, which set the initial position of the body in advance of the acceleration phase of the jump. In *Cacopsylla*, the take-off angle was 80±1 deg and in the largest species, *Psylla*, it was not significantly different at 76±6 deg, but in *Psylloopsis* the angle was shallower at 62±7 deg (Table2). These figures indicate that take-off angle is not a function of body size and mass.

Second, the rate of spin in the pitch plane was high. In *Psylla* and *Psylloopsis*, the mean rotation rates in the first 80 ms after take-off were 221±11 Hz and 199±17 Hz, respectively, but the smaller *Cacopsylla* had a higher rate of 336±14 Hz. As for take-off angles, similar rates of body spins were seen when jumping from surfaces of different orientations. Once airborne, wind resistance gradually slowed the rate of rotation in all species. The wings did not immediately open upon take-off to stabilise the body against these pitch rotations. The earliest the wings were seen to open was after

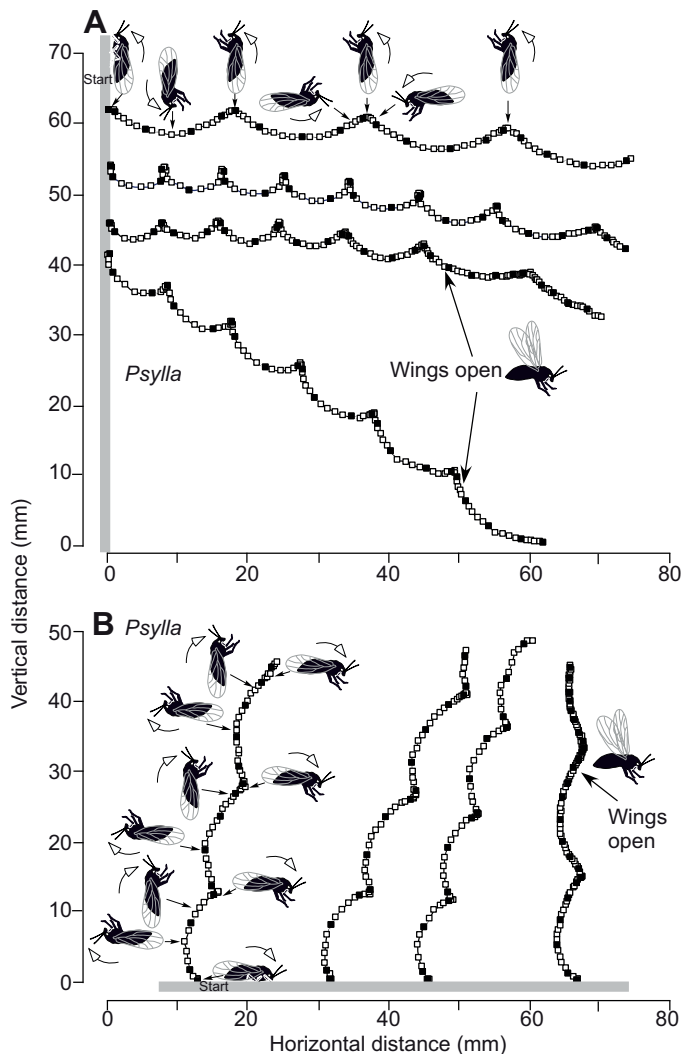


Fig. 6. Body rotations in the pitch plane after take-off from jumps by *Psylla alni*, plotted as vertical displacement against horizontal displacement; the open symbols show the position of the front of the head every 0.4 ms and the filled symbols give a time scale of every 2 ms. The cartoons show the orientation of the body at the points indicated, and the curved arrows with open heads indicate the direction of rotation. (A) Four jumps in which three *Psylla* jumped from a vertical wall (vertical, grey bar) in the chamber. In all jumps the body rotated, and in two jumps the wings were opened at the points indicated by the black arrows and began to flap. (B) Four jumps, all by the same *Psylla*, from the floor of the chamber (horizontal, grey bar). In one jump, the wings were opened (black arrow) and began to flap.

some five cycles of rotation (Fig. 6), but in many jumps the wings remained closed throughout the jump so that continuing rotation of the body resulted in landings that were not controlled. Opening of the wings was sometimes followed by flapping movements that re-oriented the body and resulted in stable forward flight.

Controlling jump trajectory

In the vast majority (209 of 211) of jumps by all three species, the head pointed downwards at take-off and the body rotated rapidly forwards in the pitch plane once airborne. Two jumps using a different strategy were performed by the same *Psyllopsis* (Fig. 7A). In these jumps, the head was raised progressively during the acceleration period so that at take-off it pointed upwards and the angle of the body relative to the horizontal was +12 deg (Fig. 7B).

By contrast, in a preceding jump by the same *Psyllopsis*, the most common strategy was used so that the head pointed downwards and the body angle at take-off was some -40 deg (Fig. 7C). At take-off, the trochanter had been rotated about the coxa by about the same amount in both jumping strategies. The difference in body orientation between the two strategies thus resulted from different movements of the femoro-tibial joints of the hind legs (Fig. 7D); in a jump with head up, the femoro-tibial joint was fully extended (180 deg) compared with achieving an angle of only half this value in jumps with the head down. Despite the similar acceleration times, jumps with the head up had a lower take-off velocity than those with the head down (Fig. 7E) and trajectories were shallower (Fig. 7F). The direction and rate of rotation once airborne were also different. When the head pointed upwards, the body spun backwards, and when downwards the body spun forwards. The pitch rate was 1360 deg s⁻¹ when the head pointed up compared with 22,270 deg s⁻¹ when it pointed down.

Synchrony of hind leg movements

The two hind legs moved in parallel planes on either side of the body and their only point of contact was between the medial edges of the coxae, which did not appear to rotate about the thorax. To propel a jump, both hind legs normally started to move together or within 0.2 ms (1 frame of the video) of each other. In some jumps, however, the movements of the hind legs were less closely synchronised. Four examples of the types and time courses of asynchrony in jumping by *Psylla* are illustrated (Figs 8, 9). In the first example (Fig. 8A), both hind legs began in contact with the ground but at -1.6 ms before take-off, the left hind leg began to move although the right hind leg did not. The trochanteral depression of the left, but not the right, hind leg is shown in frame -1.0 ms before take-off (Fig. 8A). This resulted in the left hind leg progressively raising the body from the ground, so that the right hind leg also lost contact with it, although it had not moved actively. Then, at 0.8 ms before the jump, the right hind leg was suddenly and rapidly depressed so that its tarsus regained contact with the ground. In the last 0.2 ms before take-off, the insect was therefore propelled by both hind legs, which reached the same angles of trochanteral depression and femoro-tibial extension at take-off. In the second example (Fig. 8B), the left hind leg again moved first and raised the body so that the right hind leg was lifted from the ground. This time, when the right hind leg began to move at -0.8 ms, it immediately depressed and extended almost fully, and thus only the left hind leg contributed thrust during the last 0.2 ms before take-off. In the third example (Fig. 8C), the left hind leg was the first to move at -1.8 ms and it then depressed the trochanter and extended the tibia fully in 0.4 ms. Only then did the right hind leg begin to depress, and its movements alone for the next 1.4 ms provided the thrust for the jump. In the fourth and final example (Fig. 9A,B), both hind legs started to depress at the same time, but while the left hind leg continued to depress and extend fully, further depression of the right hind leg was delayed for 0.6 ms. For the last 0.8 ms of the acceleration period, this jump was propelled by the action of a single hind leg.

In jumps such as these with such asynchronous movements of the hind legs, there were no significant differences in the take-off angles of the body or the rate of pitch rotation compared with jumps with more synchronous movements. Moreover, there was no rotation in the yaw plane, and rotation in the roll plane was not apparent. These results therefore indicate that jumping performance of *Psylla* is resilient to asynchronies of 0.4–1.0 ms, or 24–59% of the acceleration period.

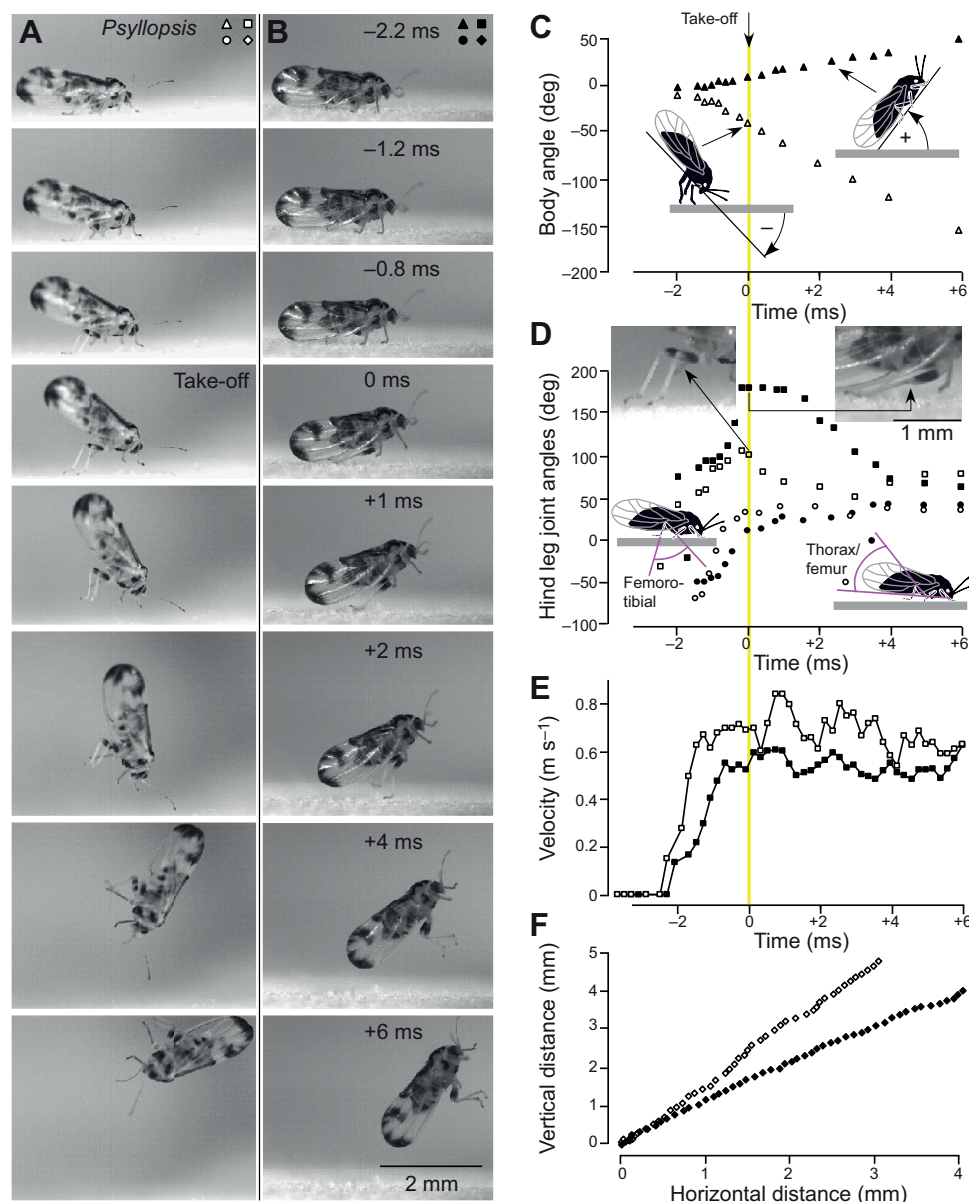


Fig. 7. Two distinct jumping strategies used sequentially by the same *Psyllopsis fraxini*. (A) Jump powered by movements of the coxo-trochanteral joints of the hind legs in which the head pointed downwards at take-off (open symbols in graphs C–F). (B) Jump powered by movements of the femoro-tibial joints in which the head pointed upwards at take-off (filled symbols in graphs C–F). (C) Graph of body angle relative to ground in a jump. In the commonly used strategy (A), the head pointed downwards at take-off and the body angles were negative; in a rarely used strategy (B), the head pointed upwards at take-off and the body angles were positive. (D) Graph of the changes in the femoro-tibial and thoraco-femoral angles. The inset frames show the different positions of the hind leg joints at take-off in the two jumping strategies. (E) Take-off velocities in both jumping strategies. (F) The trajectory of the take-off was steeper using the strategy in A compared with the strategy in B.

Jumping performance

Further features of the jumping performance were calculated from the data obtained from the high-speed images (Table 2). The mean acceleration over the whole of the take-off period in an average jump was not significantly different between *Psylla* (1060 m s^{-2}) and *Psyllopsis* (910 m s^{-2}) but was almost twice as large (1910 m s^{-2}) in the smaller *Cacopsylla*, which also had the shortest acceleration time. In their best jumps, *Psylla* and *Psyllopsis* experienced 275 g and 204 g , respectively, but *Cacopsylla* experienced more than twice as much at 637 g . The energy required to achieve these performances was, on average, $4.6 \mu\text{J}$ in *Psylla*, rising to $13.1 \mu\text{J}$ in its best jumps, and 0.8 – $1.1 \mu\text{J}$ (2.6 – $3.1 \mu\text{J}$ in their best jumps) in the other two species. The power output in an average jump by *Psylla* was 2.7 mW , rising to 13 mW in its best jumps. In *Psyllopsis*, the comparable figures were 0.6 and 3.3 mW and in *Cacopsylla* 1.2 and 7.8 mW . The force exerted by *Psylla* in an average jump was 3 mN , rising to 9.7 mN in its best jumps; in *Psyllopsis*, the comparable values were 1.1 and 3.5 mN , and in *Cacopsylla* 1.4 and 6.3 mN .

It was hard to get reliable measurements of the height and distance jumped by psyllids because their small size and tumbling motion made it difficult to distinguish jumps in which the wings were not moved from those that were eventually assisted by flapping movements of the wings.

DISCUSSION

Jumping in psyllids is propelled by rapid movements of the hind legs, which are less than 75% of the length of the body and only 10–20% longer than the other legs. They are moved in parallel planes on either side of the body by large trochanteral depressor muscles located in the metathorax. Most frequently, both hind legs are moved within 0.2 ms of each other, but jumping performance is not greatly affected when there is a delay of 1 ms between the two. These movements accelerate the body to take-off in 0.9 – 1.7 ms , depending on the body mass of the particular species. In the best jumps from the horizontal, take-off velocity reached 2.7 m s^{-1} and the trajectory was steep. Once airborne, the body spun rapidly forwards in the pitch plane at rates of 199 – 336 Hz , depending on the species. The

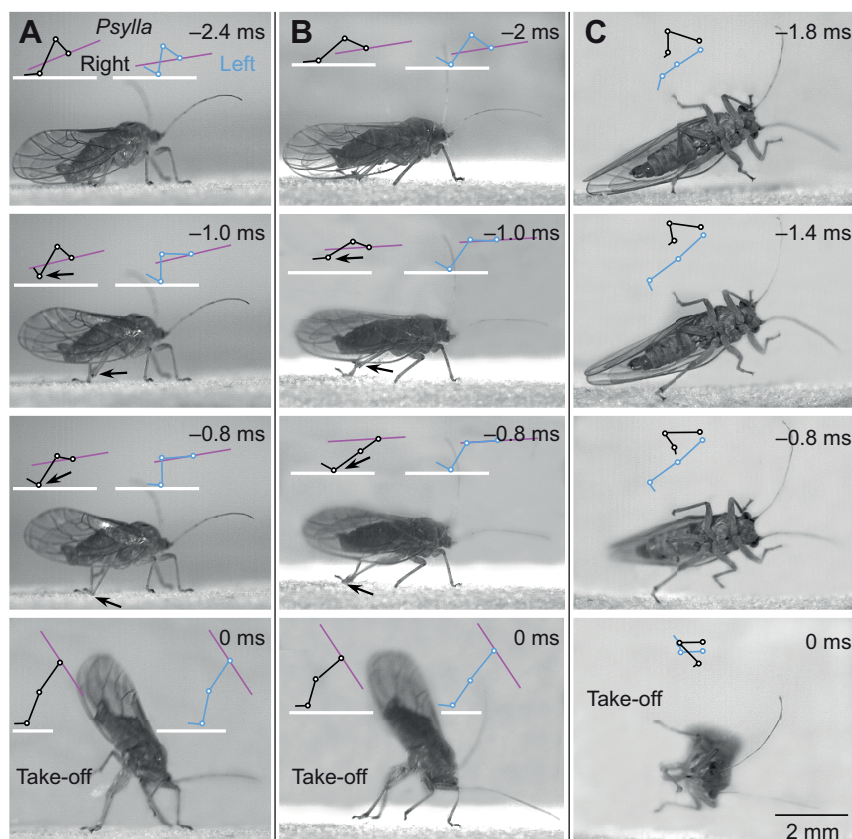


Fig. 8. Asynchrony of hind leg movements during jumping. Selected frames from three jumps by *Psylla alni* are arranged in columns A–C. A diagram on each frame shows the angles of the trochanter relative to the body, the femoro-tibial angle and the tibio-tarsal angle for each hind leg (right in black, left in blue). The pink line indicates the angle of the body relative to the horizontal. The movements of the left hind leg, which are partially obscured by the body in the initial frames in this and Fig. 9, were determined from the position of the hind tarsus, the length of the hind tibia that was visible, and knowledge of the position of the trochantero-coxal joint visible in later frames. In A and B, the ground is indicated by the horizontal white bar; in C, take-off was from the front wall of the glass chamber.

wings did not usually open to provide stabilisation during the early part of the trajectory, but some jumps eventually led directly to sustained flight. In their best jumps, a psyllid could experience a force of 637g. The largest species had an energy requirement of 13 μ J, a power output of 13 mW and exerted a ground reaction force of nearly 10 mN. The short acceleration time and the energy required for jumping indicate that direct muscle contractions could not generate these jumps (Askew and Marsh, 2002; Ellington, 1985; Josephson, 1993; Weis-Fogh and Alexander, 1977). Instead, a catapult mechanism must be used, as in many other jumping insects such as fleas (Bennet-Clark and Lucey, 1967; Sutton and Burrows, 2011), locusts (Bennet-Clark, 1975; Heitler and Burrows, 1977), froghoppers (Burrows, 2006), leafhoppers (Burrows, 2007a) and planthoppers (Burrows, 2009a).

Defining features of jumping

The characteristic features of jumping in psyllids are that the head points downwards at take-off and that once airborne the body rotates rapidly forwards in the pitch plane. Both features indicate that the force applied by the rapid depression of the hind trochanters is not passing directly through the centre of mass of the psyllid. Moreover, the angle of the take-off trajectory was consistently much higher than the 45 deg optimum for achieving the greatest translational distance of the body in a jump. The forward rotation of the body began during the acceleration period of the jump and resulted in the abdomen being raised from the ground but the head tilting closer towards it. This in turn meant that the weight of the body was being moved onto the front legs and that their support was an integral part of the propulsive mechanism for jumping. By contrast, insects as diverse as locusts and froghoppers may lift their front legs from the ground before the propulsion from the hind legs has been completed.

In psyllids, the front legs lose contact with the ground at the same time as, or even after, the hind legs. They therefore play a key role in supporting the body while thrust is applied by the hind legs. The posture adopted by psyllids as they are about to jump is strikingly similar to that of a human performing a handstand. A head-down posture is also adopted by psyllids when feeding naturally with their piercing mouthparts, which emerge ventrally between the front and middle legs (see Fig. 2A) and are pressed against the host plant and into the phloem. From this posture, the common head-down, jumping strategy would provide the most rapid escape.

The initial rate of rotation once airborne is remarkable, ranging from ~200 Hz in the larger species to more than 300 Hz in the smallest species. The rotation was limited to the pitch plane and results from application of force by the hind legs behind the centre of mass. The only insects known to exceed these rotation rates during a jump are springtails, which propel themselves by extending the forked furca at the end of their abdomen, and thus well behind their centre of mass, with resulting spin rates of 480 Hz (Christian, 1979). In pygmy mole crickets, the spin rate is above 100 Hz, but in these insects the pitch rotation is backwards (Burrows and Picker, 2010), and in flea beetles the forward spin rates range from 21 to 187 Hz in different species (Brackenbury and Wang, 1995). In froghoppers and leafhoppers, the spin rates are much lower and do not exceed 10 Hz (Brackenbury, 1996). Spinning at high rates will consume much energy that could otherwise have contributed to the forward momentum, and hence displacement of the body. In the present study, wings were not opened or flapped in the initial stages of any jumps and could not therefore contribute to stabilisation. Some jumps did, however, lead directly to stable flight later in a trajectory.

What evolutionary advantage could spinning add to jumping, or is it just a consequence of body shape? In springtails, which use an

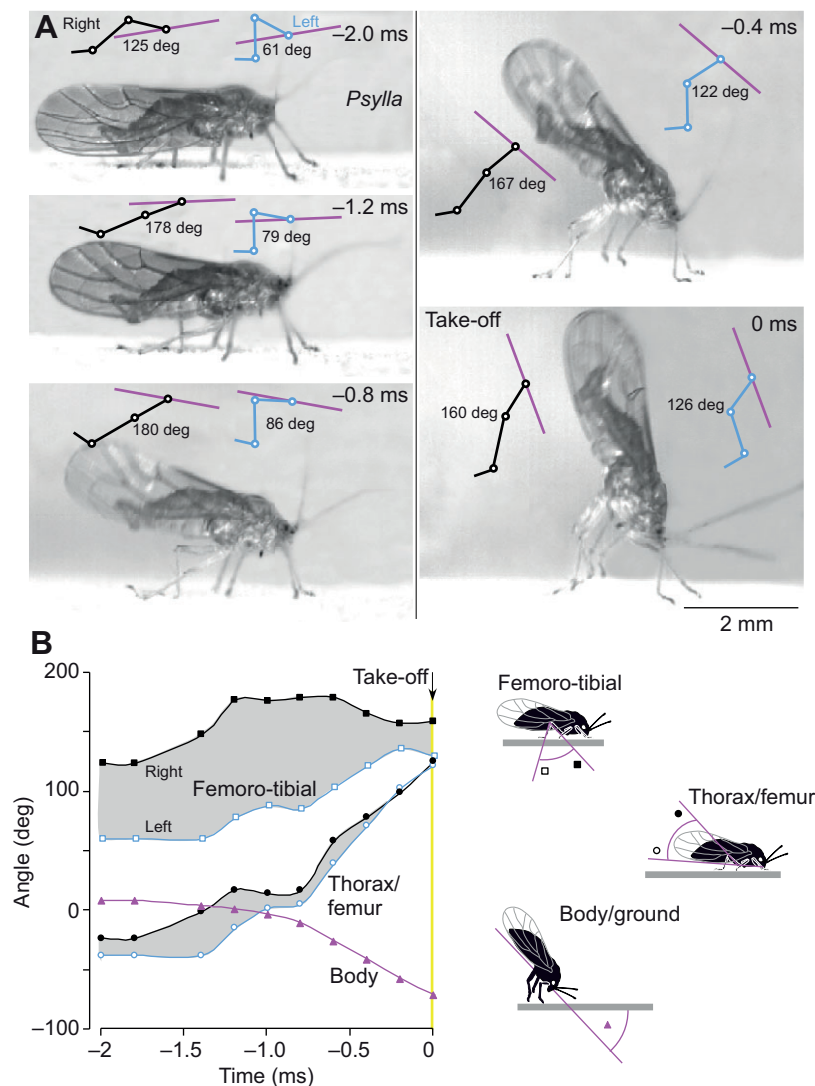


Fig. 9. Jump by *Psylla alni* powered predominantly by one hind leg. (A) Selected frames from the jump, with diagrams (as in Fig. 8) showing the progressive changes in the joint angles of the two hind legs (right in black, left in blue) and the orientation of the body (pink line). (B) Graphs of the changes in joint angles (as indicated in the cartoons on the right) of the right and left hind leg (right, filled symbols; left, open symbols). The pink triangles represent the orientation of the body.

appendage at the rear end of the body in jumping, there seems little scope in adjusting the point of force application relative to the centre of the body mass. With the use of hind legs that move at the side of the body, as in psyllids, scope for adjustment is limited by the length of the metathoracic segment relative to the centre of mass. A mechanism for varying the spin rate is, however, available to psyllids but it appears to be used rarely. In only two of 211 jumps analysed, the movements of the femoro-tibial joints were more extensive and resulted in the head pointing upwards at take-off and the resulting spin rate being greatly reduced. The mechanics of how this is achieved await determination of the natural circumstances under which psyllids will more readily use this jumping strategy.

Given that psyllids can generate jumps with little spin, why do they so frequently jump in a way that generates high spin rates? First, spinning will add to the unpredictability of the trajectory of a jump and the subsequent landing. A predator seeking to catch an airborne psyllid will find it harder to predict its position from its starting position. Second, if the spin rate can be varied, then predators will not be able to predict accurately the landing site. Such advantages as these must outweigh those where all the energy is put into achieving the highest velocity of a jump and argue in favour of psyllid jumping being a mechanism of escape from predators rather than a fast way of moving from one place to another. Potential predators are numerous and include lacewings, wasps and ladybirds.

If detected in time, a rapid jump should displace psyllids from the grasp of such predators.

Jumping performance

The jumping performance of psyllids places them firmly amongst the most accomplished of jumping insects. The acceleration time of a jump is much shorter than that of larger locusts (Bennet-Clark, 1975) and is similar to that of froghoppers (Burrows, 2006), planthoppers (Burrows, 2009a) and fleas (Sutton and Burrows, 2011). Their take-off velocities, however, fall well short of those of the first two groups, but match those of leafhoppers (Burrows, 2007a) and exceed those of fleas (Sutton and Burrows, 2011). It has not been possible to compare jumping distances because spinning psyllids are hard to distinguish from ones flapping their wings. All of the insects mentioned here use catapult mechanisms. This implies that the power-producing muscles must contract slowly before a jump, energy must then be stored in structures within the body and then released suddenly. The energy storage mechanisms are only known for a few insects and they are varied: flea beetles are suggested to use a spring in the hind femur (Furth, 1988; Furth et al., 1983); locusts use several sites, including active bending of semi-lunar springs in the femur (Bennet-Clark, 1975; Burrows and Morris, 2001; Cofer et al., 2010); froghoppers and planthoppers actively bend the metathoracic pleural arches by prolonged

contractions of trochanteral depressor muscles and then unfurl them before a jump (Burrows, 2010; Burrows et al., 2008). These arches are made of a composite of the soft, elastic protein resilin and hard cuticle (Burrows et al., 2008). The next task in psyllids must be to identify the structures that store the energy generated by the trochanteral depressor muscles and to analyse whether they are made of a composite of resilin and hard cuticle.

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REFERENCES

- Askew, G. N. and Marsh, R. L. (2002). Muscle designed for maximum short-term power output: quail flight muscle. *J. Exp. Biol.* **205**, 2153-2160.
- Bennet-Clark, H. C. (1975). The energetics of the jump of the locust *Schistocerca gregaria*. *J. Exp. Biol.* **63**, 53-83.
- Bennet-Clark, H. C. and Lucey, E. C. A. (1967). The jump of the flea: a study of the energetics and a model of the mechanism. *J. Exp. Biol.* **47**, 59-67.
- Brackenbury, J. (1996). Targetting and optomotor space in the leaf-hopper *Empoasca vitis* (Gothé) (Hemiptera: Cicadellidae). *J. Exp. Biol.* **199**, 731-740.
- Brackenbury, J. and Wang, R. (1995). Ballistics and visual targeting in flea-beetles (Alticinae). *J. Exp. Biol.* **198**, 1931-1942.
- Burrows, M. (2003). Biomechanics: frog hopper insects leap to new heights. *Nature* **424**, 509.
- Burrows, M. (2006). Jumping performance of frog hopper insects. *J. Exp. Biol.* **209**, 4607-4621.
- Burrows, M. (2007a). Kinematics of jumping in leafhopper insects (Hemiptera, Auchenorrhyncha, Cicadellidae). *J. Exp. Biol.* **210**, 3579-3589.
- Burrows, M. (2007b). Neural control and coordination of jumping in frog hopper insects. *J. Neurophysiol.* **97**, 320-330.
- Burrows, M. (2009a). Jumping performance of planthoppers (Hemiptera, Issidae). *J. Exp. Biol.* **212**, 2844-2855.
- Burrows, M. (2009b). Jumping strategies and performance in shore bugs (Hemiptera, Heteroptera, Saldidae). *J. Exp. Biol.* **212**, 106-115.
- Burrows, M. (2010). Energy storage and synchronisation of hind leg movements during jumping in planthopper insects (Hemiptera, Issidae). *J. Exp. Biol.* **213**, 469-478.
- Burrows, M. and Morris, G. (2001). The kinematics and neural control of high-speed kicking movements in the locust. *J. Exp. Biol.* **204**, 3471-3481.
- Burrows, M. and Picker, M. D. (2010). Jumping mechanisms and performance of pygmy mole crickets (Orthoptera, Tridactylidae). *J. Exp. Biol.* **213**, 2386-2398.
- Burrows, M., Hartung, V. and Hoch, H. (2007). Jumping behaviour in a Gondwanan relict insect (Hemiptera: Coleorrhyncha: Peloridiidae). *J. Exp. Biol.* **210**, 3311-3318.
- Burrows, M., Shaw, S. R. and Sutton, G. P. (2008). Resilin and chitinous cuticle form a composite structure for energy storage in jumping by frog hopper insects. *BMC Biol.* **6**, 41.
- Christian, E. (1979). The jump of the Collembola. *Zool. Jb. Physiol.* **83**, 457-490.
- Cofer, D., Cymbalyuk, G., Heitler, W. J. and Edwards, D. H. (2010). Neuromechanical simulation of the locust jump. *J. Exp. Biol.* **213**, 1060-1068.
- Crawford, D. L. (1914). A monograph of the jumping plant-lice or Psyllidae of the New World. *Bull. US Natl. Mus.* **85**, 1-182.
- Ellington, C. P. (1985). Power and efficiency of insect flight muscle. *J. Exp. Biol.* **115**, 293-304.
- Furth, D. G. (1988). The jumping apparatus of flea beetles (Alticinae) – the metafemoral spring. In *The Biology of Chrysomelidae* (ed. P. Jolivet, E. Petitpierre and T. H. Hsiao), pp. 285-297. Dordrecht: Kluwer Academic.
- Furth, D. G., Traub, W. and Harpaz, I. (1983). What makes *Blepharida* jump? A structural study of the metafemoral spring of a flea beetle. *J. Exp. Zool.* **227**, 43-47.
- Heitler, W. J. and Burrows, M. (1977). The locust jump. I. The motor programme. *J. Exp. Biol.* **66**, 203-219.
- Josephson, R. K. (1993). Contraction dynamics and power output of skeletal muscle. *Annu. Rev. Physiol.* **55**, 527-546.
- Sutton, G. P. and Burrows, M. (2011). Biomechanics of jumping in the flea. *J. Exp. Biol.* **214**, 836-847.
- Weber, H. (1929). Kopf und Thorax von *Psylla mali* Schmidb (Hemiptera-Homoptera). Eine Morphogenetische Studie. *Z. Morphol. Oekol. Tiere* **14**, 59-165.
- Weis-Fogh, T. and Alexander, R. M. (1977). The sustained power output from striated muscle. In *Scale effects in Animal Locomotion* (ed. T. J. Pedley), pp. 511-525. London: Academic Press.