

RESEARCH ARTICLE

Jumping mechanisms in gum treehopper insects (Hemiptera, Eurymelinae)

Malcolm Burrows

Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK

mb135@hermes.cam.ac.uk

SUMMARY

Jumping in a species of Australian gum treehopper was analysed from high-speed images. *Pauroeurymela amplicincta* adults and nymphs lived together in groups that were tended by ants, but only adults jumped. The winged adults with a body mass of 23 mg and a body length of 7 mm had some morphological characteristics intermediate between those of their close relatives the leafhoppers (Cicadellidae) and the treehoppers (Membracidae). They, like leafhoppers, lacked the prominent prothoracic helmets of membracid treehoppers, and their large hind coxae were linked by press studs (poppers), that are present in leafhoppers but not treehoppers. The hindlegs were only 30–40% longer than the other legs and 67% of body length. They are thus of similar proportion to the hindlegs of treehoppers but much shorter than those of most leafhoppers. Jumping was propelled by the hindlegs, which moved in the same plane as each other beneath and almost parallel to the longitudinal axis of the body. A jump was preceded by full levation of the coxo-trochanteral joints of the hindlegs. In its best jumps, the rapid depression of these joints then accelerated the insect in 1.4 ms to a take-off velocity of 3.8 ms^{-1} so that it experienced a force of almost 280 g. In 22% of jumps, the wings opened before take-off but did not flap until the gum treehopper was airborne, when the body rotated little in any plane. The energy expended was 170 μJ , the power output was 122 mW and the force exerted was 64 mN. Such jumps are predicted to propel the insect forwards 1450 mm (200 times body length) and to a height of 430 mm if there is no effect of wind resistance. The power output per mass of jumping muscle far exceeded the maximum active contractile limit of muscle and indicates that a catapult-like action must be used. This eurymelid therefore out-performs both leafhoppers and treehoppers in its faster acceleration and in its higher take-off velocity.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/216/14/2682/DC1>

Key words: locomotion, kinematics, muscle, leg movements, leaf hoppers.

Received 11 January 2013; Accepted 20 March 2013

INTRODUCTION

Jumping as a means of rapid locomotion, launching into flight, or speedy escape from threatening stimuli and predators is particularly well developed in hemipteran plant-sucking bugs. One group of these bugs (suborder Auchenorrhyncha) itself contains three major lineages (Dietrich et al., 2001) (see Fig. 1): first, the Fulgoroidea contains a wide range of forms of planthoppers in many different families; second, the Cercopoidea contains three families of froghoppers (spittle bugs). The fastest jumping insects, both in terms of their acceleration times and their take-off velocities are found in these lineages (Burrows, 2003; Burrows, 2006a; Burrows, 2009). The third lineage, the Membracoidea, contains the leafhoppers (Cicadellidae) and the treehoppers (Membracidae), which are also accomplished jumpers (Burrows, 2007b; Burrows, 2013).

Jumping in all three groups is generated by large trochanteral depressor muscles located in the thorax, which propel the rapid and simultaneous movements of the hindlegs, which are arranged beneath the body (Burrows, 2006a; Burrows, 2007b; Burrows, 2009). They all use a catapult mechanism in which the power-producing muscles contract slowly in advance of a jump, energy is stored in distortions of the skeleton and is then released suddenly. Both froghoppers and planthoppers store energy by bending parts of the internal skeleton (the pleural arches) that are made of a composite of hard cuticle and the rubber-like protein resilin (Burrows et al., 2008). In leafhoppers and treehoppers the hind coxae extend

from the midline to the lateral edges of the thorax so that there is insufficient space to accommodate large pleural arches. How energy is stored in this group is unknown.

In leafhoppers alone the two hind coxae are linked at the midline by a press stud (popper) (Burrows, 2007a; Emeljanov, 1987; Gorb, 2001). Froghoppers also have a protrusion on the hind coxa and one on the hind femur that are both covered with microtrichia and which engage with each other when the hindlegs are cocked in preparation for jumping (Burrows, 2006b). These can provide a physical constraint to leg movement during the prolonged contractions of the trochanteral depressor muscles before a jump. In planthoppers the femoral structure is a flat plate without microtrichia (Burrows, 2009), and in leafhoppers and treehoppers both structures are absent.

Within the third group, the Membracoidea, the leafhoppers (Cicadellidae) typically have an elongated and streamlined body shape but the treehoppers (Membracidae) have a distinctive body shape that is dominated by elaborations of the prothorax into forward- and backward-pointing protrusions, the embryological origin of which is not resolved (Mikó et al., 2012; Prud'homme et al., 2011; Yoshizawa, 2012). Another defining difference between these two groups is that most leafhoppers (the Ulopinae are an exception) have characteristically long hindlegs that are twice the length of the front legs (Burrows, 2007a). In sharp contrast, the treehoppers (Membracidae) have short hindlegs that are only 30–60% longer than the front legs (Burrows, 2013). When using a

catapult mechanism, the length of the hindlegs should have an impact only on the time taken to depress and extend the legs fully and hence on the distribution of the ground reaction forces over time (Burrows and Sutton, 2008). The long legged leafhoppers should therefore lose less energy in the deformation of resilient surfaces, such as flexible leaves, in comparison with treehoppers that will exert higher ground reaction forces through their shorter hindlegs.

The aim of this paper was to analyse the jumping mechanisms and performance of a closely related group within the Membracoidea, the Eurymelinae. Their jumping mechanisms are shown to have anatomical features that are intermediate between those of leafhoppers and treehoppers. The body is squat and the hindlegs are short like those of treehoppers, but their hind coxae are linked by press studs as in leafhoppers. This mixture of anatomical features results in a jumping performance that is better than that of both leafhoppers and membracid treehoppers, in terms of shorter acceleration times and higher take-off velocities.

MATERIALS AND METHODS

Pauroeurymela amplicincta (Walker) adults and nymphs were caught on Eucalyptus along Govetts Leap track near Blackheath in the Blue Mountains of NSW, Australia ($-33^{\circ}37'24.7152''\text{S}$, $150^{\circ}18'47.1852''\text{E}$). Darwin walked this same trail in 1836 (Keynes, 1988) and during his visit to this part of Australia collected this species of eurymelid which he labelled simply as being from Sydney. Today, this species is not found in Sydney but is locally common in the Blue Mountains. Darwin's specimen is in the Hope Collections in the Museum of Zoology at Oxford University, UK (Mann and Simmons, 2009). This species belongs to the order Hemiptera, suborder Auchenorrhyncha. Within this, a lineage of the Cicadellidae gave rise to the Membracidae (treehoppers), the Ulopinae and the Eurymelinae (gum treehoppers) (Dietrich et al., 2001) (Fig. 1A). The Eurymelinae group is confined to Australia, New Guinea and New Caledonia and consists of three tribes; the one to which *Pauroeurymela* belongs contains some 30 other species in 11 genera, all of which have similar body shapes (Fletcher, 2009). They are called gum treehoppers because all are found on eucalypts and most are tended by ants.

Sequential images of jumps were captured at rates of $5000\text{ images s}^{-1}$ and an exposure time of 0.05 ms, with a single Photron Fastcam 512PCI camera (Photron Europe, High Wycombe, Bucks, UK). The images were saved directly to a portable computer for later analysis. Jumps occurred spontaneously, or were encouraged by delicate mechanical stimulation with a fine paintbrush, in a chamber of optical quality glass 80 mm wide, 80 mm tall and 10 mm deep at floor level expanding to 25 mm at the ceiling. The floor was made of high-density foam (Plastazote). The camera, fitted with a 100 mm micro Tokina lens, pointed directly at the middle of this chamber, the shape of which constrained most jumps to the image plane of the camera (see supplementary material Movies 1 and 2 for jumps viewed from the side and from the front of the insect, respectively).

Selected image files were analysed with Motionscope camera software (Redlake Imaging, Tucson, AZ, USA) or with Canvas 12 (ACD Systems of America, Miami, FL, USA). A fixed point on the body just behind the hindlegs and close to the centre of mass (determined by balancing an insect on a pin) was followed in each frame. 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 from the image plane of the camera by $\pm 30^{\circ}$ deg were calculated to result in a maximum error of 10% in the measurements of joint or body angles. Peak velocity was calculated as the distance moved in a rolling three-point average of successive images and the values

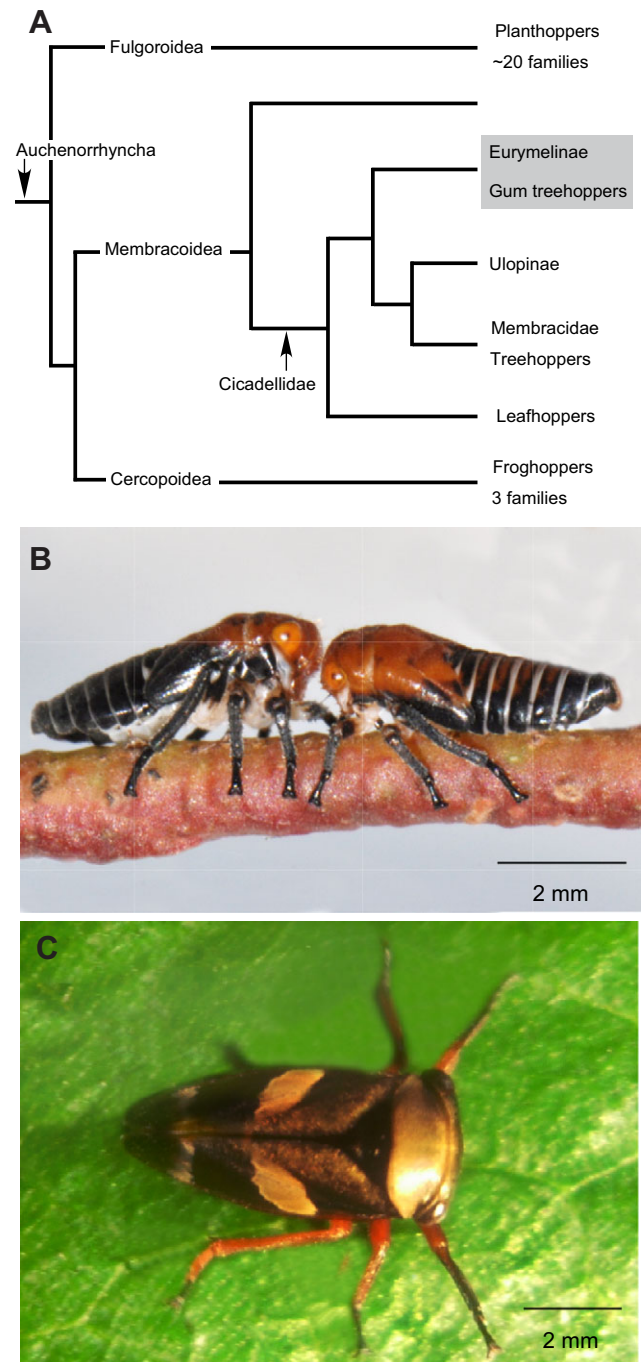


Fig. 1. (A) The relationship within the Auchenorrhyncha between the Eurymelinae, treehoppers and leafhoppers. (B) Photograph of two wingless *Pauroeurymela amplicincta* nymphs viewed from the side. (C) Photograph of a winged *P. amplicincta* adult viewed from above.

given are for the final millisecond before take-off. The time at which the hindlegs lost contact with the ground and the insect therefore took-off and became airborne was designated as time $t=0$ ms so that different jumps could be aligned and compared. The period from the first detectable movement of the hindlegs until the insect became airborne defined the acceleration time of a jump. A one-frame error in estimating both the first movement of the hindlegs and the take-off time would result in a 10% error in measuring acceleration time. A total of 40 jumps by six adults were captured with a minimum

of four jumps by each. Measurements are given as means ± s.e.m. Temperatures ranged from 24 to 30°C.

The anatomy of the hindlegs and metathorax was examined in intact insects and in insects preserved in the following ways: fixation in 5% buffered formaldehyde and subsequent storage in 70% alcohol; fixation and storage in 70% alcohol; preservation in 50% glycerol; cleared by soaking in 5% potassium hydroxide for up to a week. Colour photographs were taken with a Nikon DXM1200 digital camera attached to a Leica MZ16 (Wetzlar, Germany) stereo-microscope. Lengths of the body and parts of the legs of fixed specimens were measured to an accuracy of 0.1 mm from images captured with this camera and microscope and then projected onto a 24 in screen. Body masses were determined to an accuracy of 0.1 mg with a Mettler Toledo AB104 balance (Beaumont Leys, Leicester, UK).

RESULTS

Pauroeurymela were found living in small groups of adults and nymphs on the lower branches of young eucalyptus trees. Each group was tended by large pugnacious ants (species not identified) attracted by the honey dew secretions that the gum treehoppers provide as potential food, aptly described as ‘touching off a relationship of convenience – or appeasement – between these organisms’ (Costa, 2006). The wingless nymphs were red on the dorsal part of the head and anterior thorax, and had a black abdomen with lighter stripes at the segmental boundaries (Fig. 1B). The adults were black with lighter stripes and patches on the wings and legs with some red colouration, and a dorsal anterior part of the thorax that was lighter in colour (Fig. 1C). Both nymphs and adults lacked prothoracic helmets, the elaboration of which into posterior or anterior projections gives the membracid treehoppers their characteristic appearance (Prud’homme et al., 2011). The adults had a body mass of 23±1.6 mg (mean ± s.e.m.) and a body length of 7±0.5 mm (*N*=9, males and females lumped together, Table 1).

The hindlegs of adults were 40% longer than the front legs, so that as expressed relative to the front legs, the ratio of the three pairs of legs was 1:1.1:1.4 (front:middle:hind; Table 1). The hindlegs represented only 67% of overall body length. Expressed relative to the cube root of body mass the ratio was 1.6 (Table 1). The hindlegs of nymphs were relatively longer than the other legs, with a ratio of 1:1.1:1.7 (front:middle:hind), but proportionately were of similar length (69%) relative to body length (Table 1).

The coxae of the hindlegs were large, stiff and dark, suggesting heavy sclerotisation of the cuticle. They abutted against each other at the ventral midline and extended to the lateral edges of the metathorax (Fig. 2A,B) with which their rotation was limited to some 20 deg. At the midline, a protrusion from the medial wall of one hind coxa inserted into the medial wall of the other hind coxa and might be expected to enhance the linkage between the two hindlegs (Fig. 2C). Such a press stud or popper-like arrangement is present in leafhoppers (Burrows, 2007a) but has not been found in membracid treehoppers (Burrows, 2013). By contrast, the coxae of the front and middle legs were smaller, were separated from each other at the midline (and thus had no linking structures) (Fig. 2A), and were capable of greater rotation with their respective thoracic segments. In late instar nymphs, the hind coxae were also separated from each other at the midline by a gap of 94±9 µm (*N*=10), somewhat smaller than the width of the gap of 130±15 µm between the middle coxae. The press stud was not present on the medial walls of the hind coxae of any of the later stage nymphs that were analysed.

The hindlegs were arranged beneath the body and the orientation of the coxo-trochanteral joints constrained the movements of both to the same plane that was almost parallel to the longitudinal body axis. By contrast, the front and middle legs projected laterally and moved in separate planes closer to the dorso-ventral axis of the body. The hind trochantera were small but were capable of being levated and depressed about the coxae through angles of 120–130 deg. Levation swung the legs forwards and depression moved them backwards. When in their fully levated position they were closely opposed to the ventral surface of the thorax and tucked between it and the dorsal surface of the femora of the middle legs.

A hind femur was only 12% longer than a front femur, whereas a hind tibia was 37% longer than a front tibia. A hind tibia had a row of four to five outwardly pointing, stout spines on its lateral surface that increased distally from 200 to 400 µm in length, two more rows of six to seven thinner spines more dorsally, and rows of closely spaced hairs about 50 µm long on its medial surface (Fig. 2B, inset). The ventral surface of the tibio-tarsal joint had a semi-circular array of spines that are well placed to increase traction as thrust is applied to the ground through the hindlegs in jumping.

Kinematics of jumping

All six adults jumped readily, but none of the 20 nymphs analysed were ever seen to jump spontaneously and they could not be

Table 1. Body form of the gum treehopper *Pauroeurymela*

	Body mass (mg)	Body length (mm)	Hind leg, femur (mm)	Hind leg, tibia (mm)	Ratio of leg lengths			Hindleg length/ body length (%)	Hindleg length/ body mass ^{1/3} (mm mg ⁻¹)
					Front	Middle	Hind		
Eurymelinae									
<i>Pauroeurymela amplicincta</i>									
Adults (<i>N</i> =9)	23±1.6	7±0.5	1.2±0.09	2.0±0.2	1	1.1	1.4	67	1.6
Nymphs (<i>N</i> =5)	10.1±0.3	5±0.02	0.9±0.05	1.6±0.03	1	1	1.7	69	1.6
Cicadellidae – leafhoppers									
<i>Aphrodes makarovi</i> ¹	18.4±1.3	8.5±0.2	2.2±0.03	3.8±0.1	1	1.2	2.2	84	2.3
Ulopinae									
<i>Cephalelus angustatus</i> ²	9.2±0.6	13.4±0.4	0.8±0.02	0.9±0.5	1	1.1	1.4	20	1
Membracidae – treehoppers									
<i>Stictocephala bisonia</i> ³	26.8±4.6	7.8±0.5	1.8±0.2	2.4±0.1	1	1	1.5	69	1.8

Body length and mass, and lengths of the hind femora and tibiae in *Pauroeurymela amplicincta*; *N* indicates the number of individuals from which the measurements were taken. The ratio of leg lengths is given relative to the front legs.

Comparisons are made with members of three related lineages in the Membracoidea. The superscripts indicate the published papers from which the data were obtained: (1) long-legged leafhoppers, Cicadellidae (Burrows, 2007b); (2) short-legged Ulopinae (Burrows and Sutton, 2008); and (3) treehoppers Membracidae (Burrows, 2013).

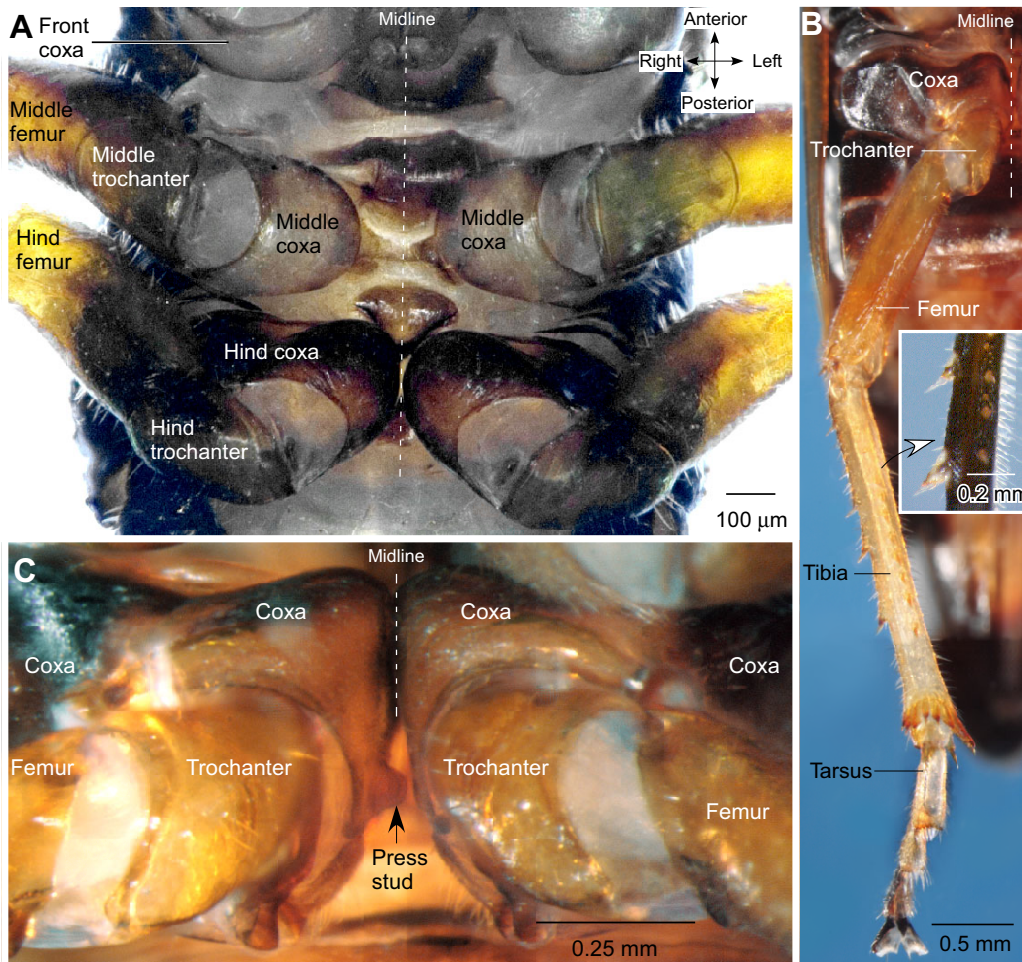


Fig. 2. Photographs to show the structure of the hindlegs and their proximal segments as viewed from the ventral surface. (A) The proximal segments of the three pairs of legs, showing the close apposition of the hind coxae compared with the greater separation of the front and middle coxae. The hind coxae are the largest and extend from the ventral midline to the lateral edges of the thorax. (B) The whole of the right hindleg viewed ventrally. The inset shows the tibial spines and rows of hairs at higher magnification. (C) A press stud (popper) between the medial edges of the two hind coxae; a protrusion from the right hind coxa (viewed ventrally and thus on the left here) engages with a socket on the left hind coxa.

encouraged to jump. Images of adult jumping movements were captured as viewed from the side when jumping from the horizontal floor of the chamber (Fig. 3), from underneath when jumping from the vertical, front glass wall (Fig. 4), and from in front when jumping from the horizontal and toward the camera (Fig. 5) (see also supplementary material Movies 1, 2). Data from all such images are incorporated into the following description on jumping kinematics.

The propulsive movements for a jump appeared to be generated by the actions of the hindlegs for the following reasons. The front and middle legs did not execute a repeated pattern of movements that indicated a consistent contribution to the generation of thrust. Moreover, they were frequently lifted from the ground before take-off occurred (Figs 3, 5). By contrast, the hindlegs performed a consistent sequence of closely synchronised movements and were always the last of the legs to leave the ground (Figs 3–5).

Prior to a jump, the angle of the longitudinal axis of the body relative to the ground was set by the positions adopted by the front and middle legs. The hindlegs were rotated forwards by full levation at their coxo-trochanteral joints. The femoro-tibial joint was not fully flexed and the tarsus was lifted slightly from the ground but placed outside the lateral edges of the body and close to the end of the abdomen. This fully levated position was then held for periods ranging from several hundred milliseconds to seconds before the hindlegs were rapidly depressed at their coxo-trochanteral joints. This movement pushed the hind femur and tibia downwards, resulting in an extension of the femoro-tibial joint and forcing the tarsus against the ground along its entire length. The two hindlegs

started these propulsive movements within the same image frame, indicating a synchronisation to within 0.2 ms or less, given the time resolution afforded by the camera frame rate of 5000 images s⁻¹. Take-off was achieved in a mean time of 1.9±0.1 ms after the first propulsive movement of the hindlegs. This time defined the period over which the body was accelerated in a jump. As the hindlegs continued to depress and extend, the body was progressively raised so that between 1.2 and 0.4 ms before a jump the front and middle legs lost contact with the ground. The hindlegs thus provided the only propulsive force during the period just before take-off. At the point of take-off, the coxo-trochanteral and femoro-tibial joints were almost fully depressed and extended, respectively, and the tarsi were also fully depressed so that both hindlegs were almost straight. The distal tips of the tarsi were the last part of the hindlegs to lose contact with the ground when the insect became airborne. The angle of the longitudinal axis of the body relative to the ground had a mean value of 27±8 deg (Table 2). The elevation angle of the jump had a steeper mean angle of 62±3 deg. Once in the air the body was stable with little rotation in the roll, pitch or yaw planes. The hindlegs often crossed, suggesting the presence of residual muscular force that no longer met with ground resistance.

In the majority of jumps the wings remained folded and thus made no contribution to the propulsive forces of the jump. In 9 of the 40 jumps analysed (22.5%), but only by two of the six insects analysed, the wings were opened and elevated before the first movements of the hindlegs. During these propulsive movements the wings depressed only through some 80 deg by the time of take-off (Fig. 5).

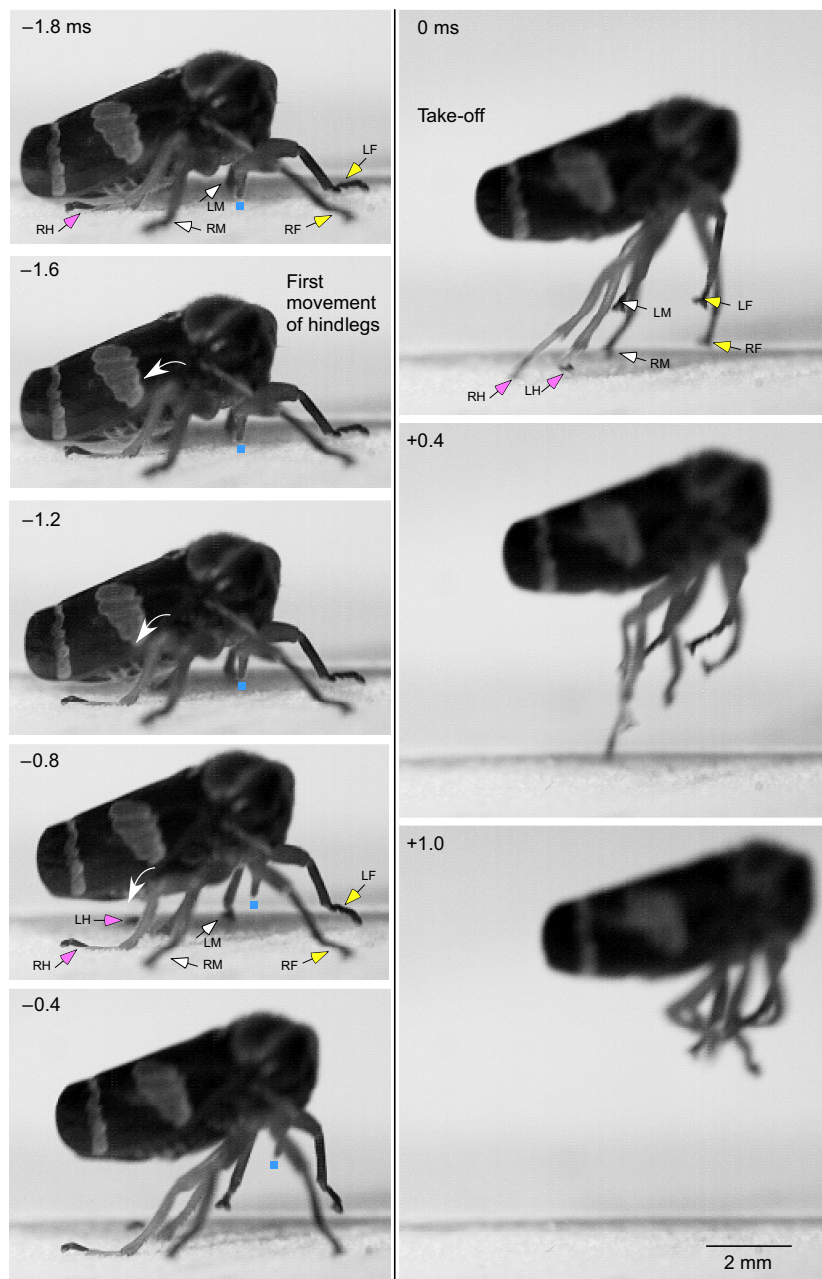


Fig. 3. Jump by an adult from a horizontal surface, viewed from the side and captured at $5000 \text{ images s}^{-1}$, with an exposure of 0.05 ms . Selected images at the times indicated are arranged in two columns with the bottom right-hand corner giving a constant point of reference. The first movements of the hindlegs occurred 1.6 ms before take-off at time 0 ms . In this jump the wings remained folded. In this and subsequent figures the legs are labelled as follows; left front (LF) and right front (RF) by arrows with yellow heads, left middle (LM) and right middle (RM) by arrows with white heads, and left hind (LH) and right hind (RH) by arrows with pink heads. The blue square indicates the tip of the piercing mouthparts, which is visible in the left-hand column.

Jumping performance

Take-off velocity was measured as a rolling three-point average from successive frames, and therefore at 0.2 ms intervals, just before take-off. The mean of means velocity of the six adults analysed was $2.7 \pm 0.1 \text{ ms}^{-1}$, with the best jump achieving a take-off velocity of 3.8 ms^{-1} . The jumping performance could be calculated from the kinematic data (Table 2). Acceleration was on average 1420 ms^{-2} but in the best jump reached 2710 ms^{-2} so that a force of $277g$ was experienced. The energy required to achieve this best performance was $170 \mu\text{J}$, the power output was 122 mW and the force exerted was 64 mN . Assuming that the trochanteral depressor muscles of the hindlegs constitute about 10% of the body mass, as in froghoppers and the planthopper *Issus* (Burrows, 2006a; Burrows, 2009), the power per muscle mass was $46,900 \text{ W kg}^{-1}$ in the best jump. This value was higher than those recorded in the best jumps by cicadellid leafhoppers, in the Ulopinae and in membracid treehoppers (Table 2).

To estimate the distance and height of a jump, it was assumed that the body acted like a small projectile as described by Eqns 1 and 2 (Alexander, 1968):

$$s = v \cos \theta (2v \sin \theta / 9.81), \quad (1)$$

$$h = (v \sin \theta)^2 / (2 \times 9.81), \quad (2)$$

where s is the distance jumped, h is the maximum height reached, v is velocity at take-off and θ is the take-off angle.

Inserting data from the kinematics (Table 2) into these equations indicates that the best jumps would propel the insect a forward distance of 1450 mm , or 200 times its body length, and to a height of 430 mm , more than 60 times its body length. In an average jump (mean of means of the jumps of six adults) the forward distance was predicted to be 600 mm and the height 290 mm .

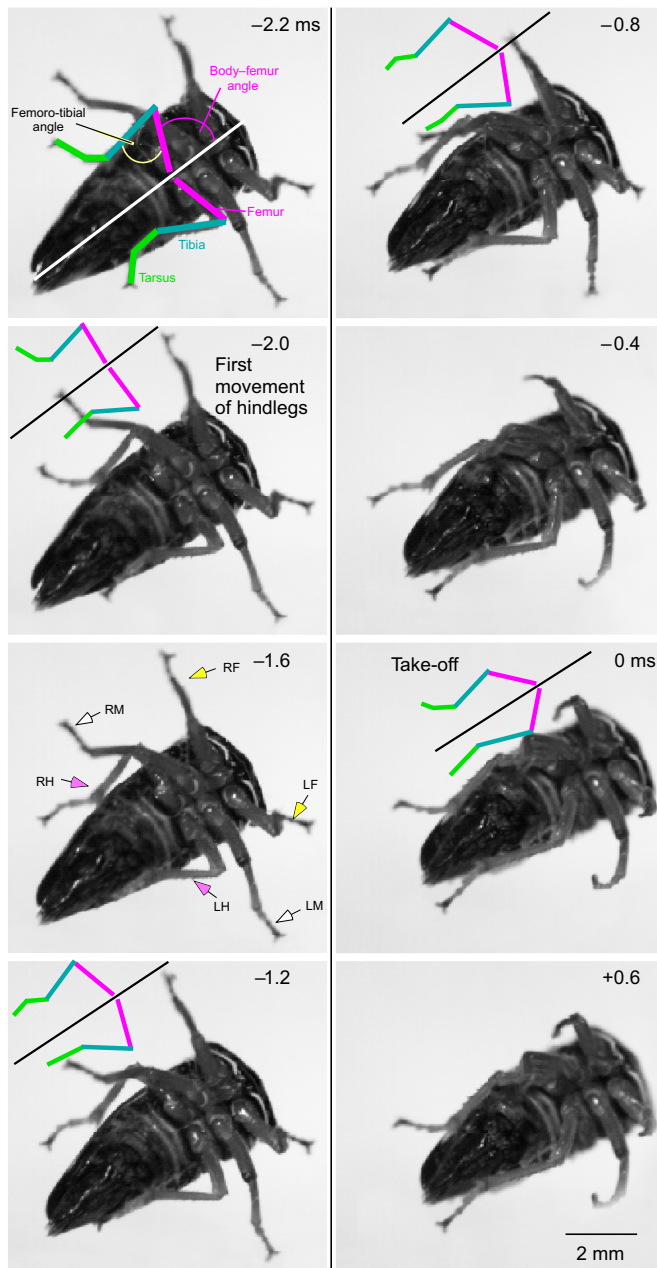


Fig. 4. Jump from a vertical surface, viewed from underneath and captured at 5000 images s^{-1} , with an exposure of 0.05 ms. In the first image at -2.2 ms the hindlegs were fully levated and were held tucked between the middle legs and the ventral surface of the body. Both hind trochanters were then rapidly depressed and the femoro-tibial joints were extended. The stick diagrams show the movements of the hind femora (pink), tibiae (blue) and tarsi (green).

DISCUSSION

Jumping performance

The jumping performance of *Pauroeurymela* outstrips that of any leafhopper, Ulopinae, and membracid treehopper so far analysed, as judged by two criteria. First, it takes less than 2 ms to accelerate the body to take-off, a time that is matched only by the Ulopinae that have short hindlegs. By contrast, long-legged leafhoppers and short-legged membracid treehoppers both take more than twice as long to take-off. It is to be expected that leafhoppers with long

hindlegs would take longer to depress these legs fully. The advantage of slower movements of long legs is that the ground reaction forces they exert are reduced so that they should lose less energy when jumping from compliant leaves (Burrows and Sutton, 2008) as opposed to jumping from the harder stems favoured by both membracid and gum treehoppers. The fast acceleration of *Pauroeurymela* compared with membracid treehoppers is less easily explained, because the hindlegs are of similar proportions both relative to its other legs and to its body length. The body mass of some treehoppers can be larger but the proportion of body mass devoted to the jumping muscles remains similar. The second criterion is take-off velocity, which can reach 3.8 ms^{-1} in the best jumps by *Pauroeurymela* and is thus higher than any recorded in either leafhoppers or membracid treehoppers. The latter treehoppers may be slowed by the increased wind resistance offered by elaborations of their prothoracic helmets that are not present in the gum treehopper analysed here.

This comparison of performance has considered only those jumps in which the wings were not moved. In *Pauroeurymela*, no jumps were seen to be preceded by repeated flapping movements of the wings, as they frequently are in some membracid treehoppers (Burrows, 2013). In the 22% of jumps in which the wings were opened before a jump, a wing beat cycle was not completed before the eurymelid became airborne. In all related groups, jumps could launch a flight but the complete trajectory of a jump could also be completed without movements of the wings. In the heavier membracid treehoppers the wings could be flapped several times before take-off but the thrust provided by the hindlegs was causal in achieving take-off (Burrows, 2013). The conclusion is that wing movements do not contribute to acceleration at take-off, but that jumps propelled by movements of the hindlegs may lead smoothly to flight powered by wing movements.

By treating the body as a simple projectile, the best jump can be calculated to propel *Pauroeurymela* forward a distance of almost 1.5 m and to height of 430 mm. These calculations ignore the effects of wind resistance, and it is likely that small insects of this size will lose some 25% of their jumping range as a result of drag (Bennet-Clark and Alder, 1979; Vogel, 2005).

Body form

Pauroeurymela has a body shape similar to that of other eurymelids, especially of the tribe to which it belongs (Fletcher, 2009). It seems reasonable to suppose that the characteristics associated with jumping that are described here are representative of the broader subfamily. *Pauroeurymela* has some anatomical features related to jumping in common with its close relatives the cicadellid leafhoppers and the membracid treehoppers, but it also has structures that are a mixture of those present in one but not the other group. All three groups have large hind coxae that extend from the midline to the lateral edges of the metathorax, seemingly to provide a stable base from which the rapid and simultaneous depression of both hind trochanters can propel jumping. If the two hindlegs were to move at different times then the body would spin rapidly in the yaw plane at take-off (Sutton and Burrows, 2010). *Pauroeurymela* adds further stability to the hind coxae by a press stud (popper) that links both at the midline. This structure is found in adult cicadellid leafhoppers, but not in nymphal leafhoppers or in membracid treehoppers of any stage. The fact that membracid treehoppers and nymphal stages of leafhoppers can still jump well without such a structure suggests that its presence is not essential.

Pauroeurymela has short hindlegs that are only 30–40% longer than the other legs and represent only 67% of body length. They

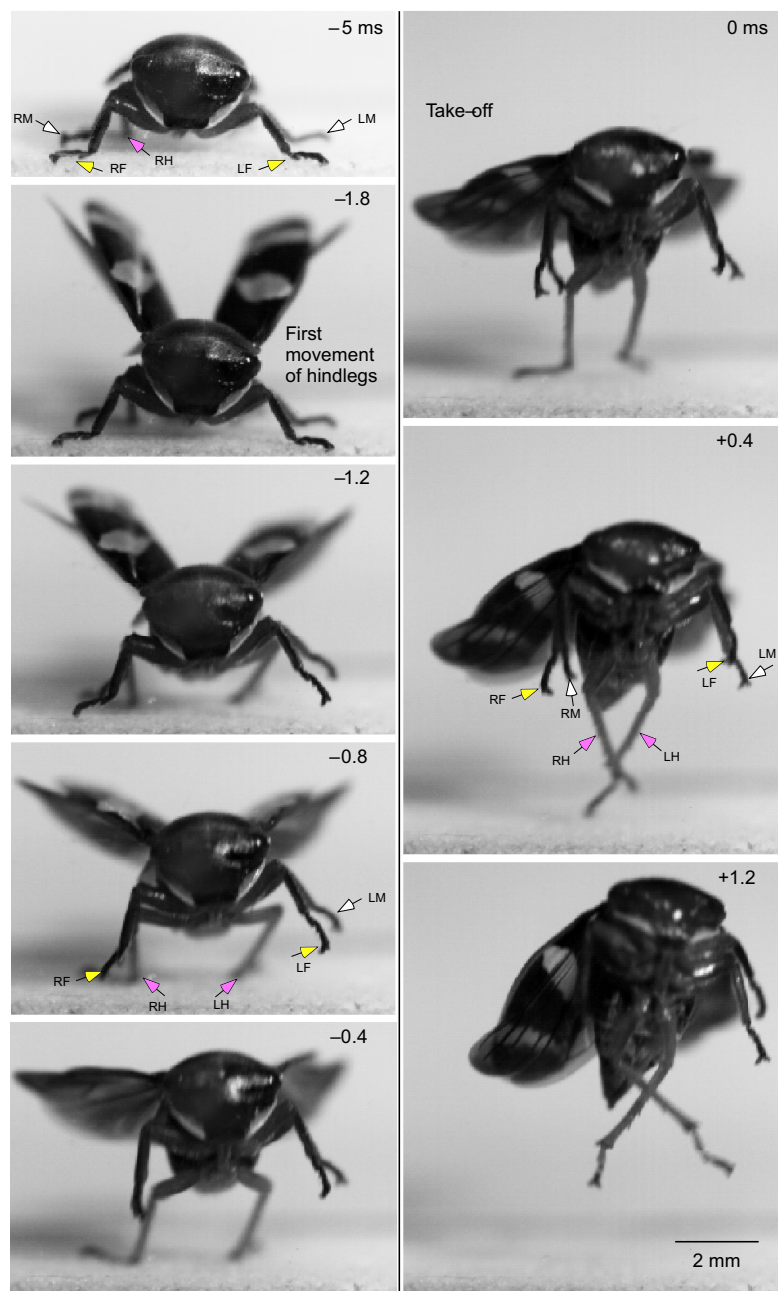


Fig. 5. Jump by an adult from a horizontal surface and toward the camera, captured at $5000 \text{ images s}^{-1}$ and with an exposure of 0.05 ms. The wings were opened and elevated before the first movement of the hindlegs began at -1.8 ms . As the hindlegs were depressed and extended, the wings were also depressed, but at take-off they had not completed their first cycle of depression.

are thus of similar proportions to those of membracid treehoppers and the Ulopinae (Burrows and Sutton, 2008), but very different from the long hindlegs of cicadellid leafhoppers, which are more than twice as long as the front legs and almost as long as the body (Burrows, 2007a; Burrows, 2007b). These differences are largely attributable to the lengths of the hind femora and tibiae. Those of *Pauroeurymela* are comparable in length to those of a membracid treehopper of similar body length, but are only half as long as those of an equivalently sized cicadellid leafhopper. The spines on the hind tibiae have characteristics intermediate with the more prominent rows of spines of cicadellid leafhoppers and of the sparse but larger spines of membracid treehoppers. Furthermore, in *Pauroeurymela*, the hindlegs expressed as a ratio relative to the cube root of body mass have a value of 1.6, closer to that in the treehopper *Stictocephala* but very different from that in both short- and long-legged leafhoppers (Table 1).

Jumping mechanisms

What mechanisms does *Pauroeurymela* use to generate these jumping performances? If it devotes 10% of its body mass to jumping muscles, as do froghoppers (Burrows, 2006a) and planthoppers (Burrows, 2009), then the power requirements for the best jumps, calculated from the observed kinematics, would be $46,900 \text{ W kg}^{-1}$ of muscle. In several hemipteran bugs the best values range from $10,000 \text{ W kg}^{-1}$ in Ulopinae to $10,400 \text{ W kg}^{-1}$ in treehoppers to $13,650 \text{ W kg}^{-1}$ in leafhoppers (Table 2), but reach much higher levels in the champion jumping froghopper *Philaeenus* ($114,500 \text{ W kg}^{-1}$) (Burrows, 2006a) and the planthopper *Issus* ($160,300 \text{ W kg}^{-1}$) (Burrows, 2009). Such outputs are far beyond the maximum active contractile limit of normal muscle; direct contraction of the muscles would only produce power outputs of between 250 and 500 W kg^{-1} (Askew and Marsh, 2002; Ellington, 1985; Josephson, 1993; Weis-Fogh and Alexander, 1977). The real

Table 2. Jumping performance of *Pauroeurymela*

	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>)	Power/kg muscle
Formula						$f=v/t$	$g=f/9.81$	$E=0.5mv^2$	$p=E/t$	$F=mf$	$p/(0.11m)$
Units	mg	ms	m s ⁻¹	deg	deg	m s ⁻²	<i>g</i>	μJ	mW	mN	W kg ⁻¹
Eurymelinae											
<i>Pauroeurymela ampicincta</i>											
Average (<i>N</i> =6)	23.0±1.6	1.9±0.1	2.7±0.1	62±3	27±8	1420	145	84	44	33	17,440
Best	23.6	1.4	3.8	50	14	2710	277	170	122	64	46,900
Cicadellidae – leafhoppers											
<i>Aphrodes makarovi</i> ¹											
Average (<i>N</i> =5)	18.4±1.3	4.4±0.2	2.5±0.1	37±4	37±5	570	58	58	13	11	6460
Best	18	2.8	2.9	37	41	1040	106	76	27	19	13,650
Ulopinae											
<i>Cephalelus angustatus</i> ²											
Average (<i>N</i> =6)	9.2±0.6	2.1±0.1	1.6±0.2	56±3	15±2	762	78	12	6	7	5540
Best	10	2	2	50	10	1000	102	20	10	10	10,000
Membracidae - treehoppers											
<i>Stictocephala bisonia</i> ³											
Average (<i>N</i> =2)	26.8±4.6	3.6±0.1	2.1±0.2	51±4	16±1	580	59	59	16	16	5570
Best	28	3.5	2.7	54	15	770	79	102	29	22	10,400

The jumping performance of *Pauroeurymela* compared with that of members of three related lineages in the Membracoidea: (1) long-legged leafhoppers, Cicadellidae (Burrows, 2007b); (2) short-legged Ulopinae (Burrows and Sutton, 2008); and (3) treehoppers Membracidae (Burrows, 2013).

Data in the five columns on the left are the mean of means ± s.e.m. for the performance in (*N*) individuals of each species and for the best performance of a particular individual. The calculated values in the five columns on the right are derived from these measured data.

mass of the jumping muscle in *Pauroeurymela* may have been underestimated by extrapolation from the measured values in froghoppers. Calculations were therefore made of the power required to meet the observed kinematic demands by the best jumps of *Pauroeurymela*, assuming that the jumping muscle represented larger percentages of total body mass. If the jumping muscle were to represent 50% of body mass, the requirements for a best jump would still exceed the maximum performance of muscle by a factor of 20, and if the body consisted entirely of jumping muscle the requirements would still be 10 times higher. Jumping in *Pauroeurymela* must therefore involve a power amplification mechanism such as could be provided by a catapult. This is the mechanism proposed for fleas (Bennet-Clark and Lucey, 1967) and demonstrated to be used by locusts (Bennet-Clark, 1975) and some other hemipteran bugs. Electrical recordings from the jumping muscles of froghoppers (Burrows, 2007c), leafhoppers (Burrows, 2007a) and the planthopper *Issus* (Burrows and Bräunig, 2010) show that they contract in advance of the rapid propulsive movements of the hindlegs. In froghoppers and *Issus* the slow contractions of these muscles bend internal skeletal structures (pleural arches) that are built of a composite of hard cuticle and the rubber-like protein resilin. The storage mechanisms in all members of this lineage of the Cicadellidae remain to be determined.

Why do only the adults jump?

Winged adults and wingless nymphs of *Pauroeurymela* live together in groups attended by ants on the low branches of eucalyptus trees. This paper has shown the ability of adults to jump with speed and power, but observations of many nymphs failed to find any that jumped. Is there a physical reason that might explain why nymphs are unable to jump? Their hindlegs, relative to the other legs, were longer than those of adults, but were of similar proportions relative to body length. Unlike the hindlegs of adults, however, they lacked a press stud linking the medial surfaces of the two coxae. Indeed the hind coxae were separated by a gap at the midline in much the same arrangements as for the front and middle legs. This might

indicate that the hind coxae do not provide a stable base from which the more distal parts of the hindlegs can propel jumping, as they do in adults. By contrast, nymphal leafhoppers, that lead solitary but mobile lives, also lack the press stud on their hind coxae but nevertheless jump well (Burrows, 2007a). Can the absence of jumping by *Pauroeurymela* nymphs, which seems to be widespread amongst other gum treehopper nymphs (Fletcher, 2009), be more readily explained by the ecology of their group living? If they were to jump, the likely result is that they would fall to the ground from the position of the groups at the axils of branches, because their descent would be unlikely to be broken by landing on leaves. Without wings and the ability to fly, recovering their position amongst the sparsely spaced groups attended by ants that might repel them would be problematical. For larval leafhoppers, by contrast, jumping from leaves means that the probability of landing on other leaves before reaching the ground would be higher. Moreover, if all else fails, they need only to regain a suitable feeding site and not a specific site where the potentially protective ants await. Why then do the adults themselves jump instead of relying on the potential protection from predators afforded by the ants? The answer might lie in the need to disperse, either to establish new colonies or to find mates from a different gene pool. On this basis, therefore, an important aspect of jumping is to launch into flight, with the need to avoid predators being reduced by the attending ants.

ACKNOWLEDGEMENTS

I thank Steve Simpson for the hospitality of his laboratory and for his help along with Swidi Ott, Steve Rogers and Darron Cullen in collecting these insects. All provided many helpful suggestions during the experimental work. I also thank Murray Fletcher for his help in identifying these bugs.

COMPETING INTERESTS

No competing interests declared.

FUNDING

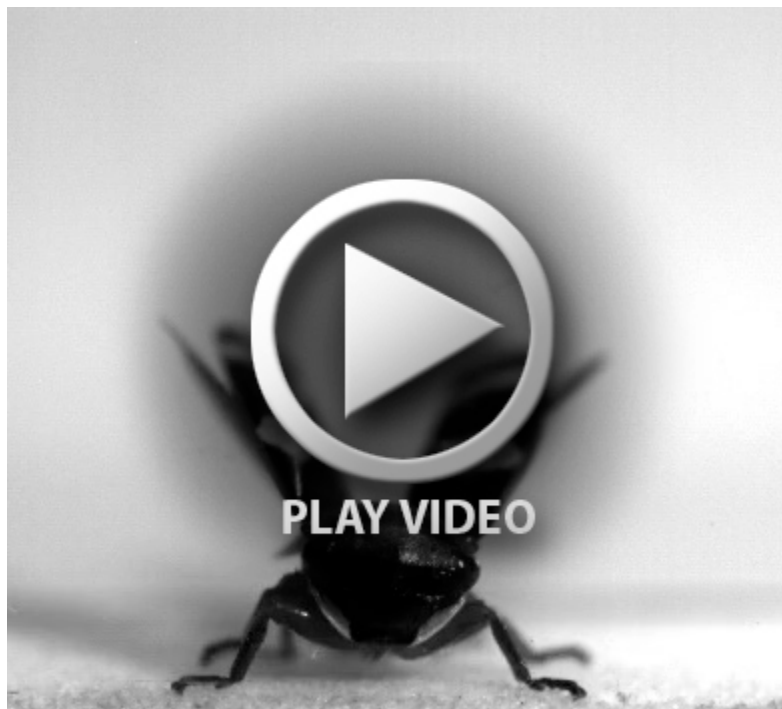
This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

REFERENCES

- Alexander, R. M.** (1968). *Animal Mechanics*. London: Sidgwick and Jackson.
- 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 Alder, G. M.** (1979). The effect of air resistance on the jumping performance of insects. *J. Exp. Biol.* **82**, 105-121.
- 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.
- Burrows, M.** (2003). Biomechanics: froghopper insects leap to new heights. *Nature* **424**, 509.
- Burrows, M.** (2006a). Jumping performance of froghopper insects. *J. Exp. Biol.* **209**, 4607-4621.
- Burrows, M.** (2006b). Morphology and action of the hind leg joints controlling jumping in froghopper insects. *J. Exp. Biol.* **209**, 4622-4637.
- Burrows, M.** (2007a). Anatomy of the hind legs and actions of their muscles during jumping in leafhopper insects. *J. Exp. Biol.* **210**, 3590-3600.
- Burrows, M.** (2007b). Kinematics of jumping in leafhopper insects (Hemiptera, Auchenorrhyncha, Cicadellidae). *J. Exp. Biol.* **210**, 3579-3589.
- Burrows, M.** (2007c). Neural control and coordination of jumping in froghopper insects. *J. Neurophysiol.* **97**, 320-330.
- Burrows, M.** (2009). Jumping performance of planthoppers (Hemiptera, Issidae). *J. Exp. Biol.* **212**, 2844-2855.
- Burrows, M.** (2013). Jumping mechanisms of treehopper insects (Hemiptera, Auchenorrhyncha, Membracidae). *J. Exp. Biol.* **216**, 788-799.
- Burrows, M. and Bräunig, P.** (2010). Actions of motor neurons and leg muscles in jumping by planthopper insects (Hemiptera, Issidae). *J. Comp. Neurol.* **518**, 1349-1369.
- Burrows, M. and Sutton, G. P.** (2008). The effect of leg length on jumping performance of short- and long-legged leafhopper insects. *J. Exp. Biol.* **211**, 1317-1325.
- Burrows, M., Shaw, S. R. and Sutton, G. P.** (2008). Resilin and chitinous cuticle form a composite structure for energy storage in jumping by froghopper insects. *BMC Biol.* **6**, 41.
- Costa, J. T.** (2006). *The Other Insect Societies*. Cambridge, MA: Belknap Press of Harvard University Press.
- Dietrich, C. H., Rakitov, R. A., Holmes, J. L. and Black, W. C., 4th** (2001). Phylogeny of the major lineages of Membracoidea (Insecta: Hemiptera: Cicadomorpha) based on 28S rDNA sequences. *Mol. Phylogenet. Evol.* **18**, 293-305.
- Ellington, C. P.** (1985). Power and efficiency of insect flight muscle. *J. Exp. Biol.* **115**, 293-304.
- Emeljanov, A. F.** (1987). Phylogeny of Cicadina (Homoptera, Cicadina) according to data on comparative morphology. (In Russian). *Trudy Vsesoiuznogo Entomologicheskogo Obschestva* **69**, 19-109.
- Fletcher, M. J.** (2009). Identification keys and checklists for the leafhoppers, planthoppers and their relatives occurring in Australia and neighbouring areas (Hemiptera: Auchenorrhyncha). <http://www1.dpi.nsw.gov.au/keys/leafhop/eurytelinae/eurytelini.htm>.
- Gorb, S.** (2001). *Attachment Devices Of Insect Cuticle*. Dordrecht: Kluwer Academic Publishers.
- Josephson, R. K.** (1993). Contraction dynamics and power output of skeletal muscle. *Annu. Rev. Physiol.* **55**, 527-546.
- Keynes, R. D.** (1988). *Charles Darwin's Beagle Diary*. Cambridge, UK: Cambridge University Press.
- Mann, D. J. and Simmons, Z.** (2009). The Hope Entomological Collections. *Antenna* **33**, 34-38.
- Mikó, I., Friedrich, F., Yoder, M. J., Hines, H. M., Deitz, L. L., Bertone, M. A., Seltmann, K. C., Wallace, M. S. and Deans, A. R.** (2012). On dorsal prothoracic appendages in treehoppers (Hemiptera: Membracidae) and the nature of morphological evidence. *PLoS ONE* **7**, e30137.
- Prud'homme, B., Minervino, C., Hocine, M., Cande, J. D., Aouane, A., Dufour, H. D., Kassner, V. A. and Gompel, N.** (2011). Body plan innovation in treehoppers through the evolution of an extra wing-like appendage. *Nature* **473**, 83-86.
- Sutton, G. P. and Burrows, M.** (2010). The mechanics of azimuth control in jumping by froghopper insects. *J. Exp. Biol.* **213**, 1406-1416.
- Vogel, S.** (2005). Living in a physical world II. The bio-ballistics of small projectiles. *J. Biosci.* **30**, 167-175.
- 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.
- Yoshizawa, K.** (2012). The treehopper's helmet is not homologous with wings (Hemiptera: Membracidae). *Syst. Entomol.* **37**, 2-6.



Movie 1. A jump by *Pauroeurymela amplicincta* captured at 5000 frames s^{-1} and replayed at 10 frames s^{-1} . The insect is viewed from the side as it jumps from the floor of the experimental chamber. See Fig. 3.



Movie 2. A side view of a jump by *Pauroeurymela amplicincta* captured at 5000 frames s^{-1} and replayed at 10 frames s^{-1} as it jumps toward the camera and moves its wings. See Fig. 5.