

RESEARCH ARTICLE

Jumping mechanisms of treehopper insects (Hemiptera, Auchenorrhyncha, Membracidae)

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SUMMARY

The kinematics and jumping performance of treehoppers (Hemiptera, Auchenorrhyncha, Membracidae) were analysed from high speed images. The eight species analysed had an 11-fold range of body mass (3.8–41 mg) and a 2-fold range of body length (4.1–8.4 mm). Body shape was dominated by a prothoracic helmet that projected dorsally and posteriorly over the body, and in some species forwards to form a protruding horn. Jumping was propelled by rapid depression of the trochantera of the hindlegs. The hindlegs were only 30–60% longer than the front and middle legs, and 47–94% the length of the body in different species. They were slung beneath the body and moved together in the same plane. In preparation for a jump, the hindlegs were initially levated and rotated forwards so that the femora were pressed into indentations of the coxae. The tibiae were flexed about the femora and the tarsi were placed on the ground directly beneath the lateral edges of the abdomen. Movements of the front and middle legs adjusted the angle of the body relative to the ground, but for most treehoppers this angle was small, so that the body was almost parallel to the ground. The rapid depression of the hindlegs accelerated the body to take-off in 1.2 ms in the lighter treehoppers and 3.7 ms in the heavier ones. Take-off velocities of $2.1\text{--}2.7\text{ m s}^{-1}$ were achieved and were not correlated with body mass. In the best jumps, these performances involved accelerations of $560\text{--}2450\text{ m s}^{-2}$ (g forces of 47–250), an energy expenditure of $13.5\text{--}101\text{ }\mu\text{J}$, a power output of $12\text{--}32\text{ mW}$ and exerted a force of $9.5\text{--}29\text{ mN}$. The power output per mass of muscle far exceeds the maximum active contractile limit of normal muscle. Such requirements indicate that treehoppers must be using a power amplification mechanism in a catapult-like action. Some jumps were preceded by flapping movements of the wings, but the propulsive movements of the hindlegs were crucial in achieving take-off.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/216/5/788/DC1>

Key words: kinematics, locomotion, muscle, biomechanics, insect.

Received 31 July 2012; Accepted 5 November 2012

INTRODUCTION

Jumping in many insects is propelled by the rapid movements of the hind pair of legs, although other parts of the body may be used by some groups. Across the insects that have been studied, two mechanical arrangements of the hindlegs have been found that constrain the mechanisms of jumping (Sutton and Burrows, 2008; Sutton and Burrows, 2010). In the first type, the hindlegs move in planes laterally displaced on either side of the body, as exemplified by locusts (Bennet-Clark, 1975) or fleas (Bennet-Clark and Lucey, 1967). In the second, an undercarriage arrangement is used, in which the hindlegs push out in the same, almost horizontal plane beneath the body. Both arrangements occur within the four sub-orders of the Hemiptera that contain many prodigious jumpers. In three of these groups the hindlegs move in separate planes at the side of the body: Coleorrhyncha (Burrows et al., 2007); Heteroptera (Burrows, 2009b); Sternorrhyncha (Burrows, 2012).

The most accomplished and numerous jumpers are found in the fourth sub-order, Auchenorrhyncha, and these have their hindlegs underneath the body. This is probably not a monophyletic group as it contains lineages that differ in many characters, and particularly in jumping mechanisms. The classification of the higher groups is therefore currently in some flux, but three groupings can be recognised. The reigning world champions of insect jumping are

found in the superfamily Cercopoidea, the froghoppers (spittle bugs) (Burrows, 2003; Burrows, 2006a), and in the superfamily Fulgoroidea, the planthoppers (Burrows, 2009a), even though the anatomical arrangements of the proximal joints of the hindlegs and of the muscles powering the jumps are different in these two groups (Burrows, 2006b; Burrows and Bräunig, 2010). Both the froghopper, *Philaenus*, and the planthopper, *Issus*, accelerate in less than 1 ms to a take-off velocity of 4.7 and 5.5 m s^{-1} , respectively, experiencing forces of $550\text{--}719\text{ g}$. These outstanding performances are achieved by using a catapult mechanism in which force is developed by the slow contraction of huge thoracic muscles whilst the motive hindlegs remain stationary. The energy produced by these contractions is stored by bending paired skeletal structures in the thorax that are a composite of hard cuticle and the rubbery protein resilin (Burrows, 2010; Burrows et al., 2008). The stored energy is then suddenly released to power the rapid movements of the hindlegs.

The third and final group within the Auchenorrhyncha is the superfamily Membracoidea, which contains the leafhoppers and the treehoppers. Most leafhoppers, Cicadellidae, have characteristically long hindlegs that are 200% longer than the front legs, but one group has shorter hindlegs that are only 40% longer than the front legs (Burrows and Sutton, 2008). The long- and short-legged species

achieve similar take-off velocities of $2\text{--}2.5\text{ m s}^{-1}$ by using catapult mechanisms. The differences in leg length lead to different acceleration times, which in turn lead to different ground reaction forces, suggesting adaptations for jumping from surfaces of different compliances. Many of these small bugs are also streamlined like bullets, which is likely to minimise air resistance during take-off and when airborne. A possible lineage of the leafhoppers (Wood, 1993) is the treehoppers within the family Membracidae. They may have originated in tropical South America, with a few lineages diversifying into the cooler Nearctic region into a few thousand species. Only one lineage has reached the Palearctic, generating just a few species. The head is often flattened at the front and the overall body shape is dominated by a prothoracic structure called a helmet (Prud'homme et al., 2011). This can form a backward projection over the body and in different species can also be elaborated into a prominent dorsal or anterior projection. These features might be expected to influence take-off velocity by increasing air resistance.

To determine what effect the distinctive yet diverse body shapes of membracids has on jumping performance, this paper analyses the jumping kinematics and mechanisms of eight species of treehoppers. They share with the long- and short-legged leafhoppers (Burrows, 2007a; Burrows and Sutton, 2008) a similar construction of the proximal joints of their hindlegs, but the overall length of the hindlegs is no more than 60% greater than the other legs and is always less than the body length. Take-off velocities are similar across species of markedly different body sizes and are higher than those of all but a few leafhoppers. Jumping must be generated by catapult-like mechanisms if the measured energy requirements are to be met. Flapping movements of the wings may precede take-off,

but the propulsive movements of the hindlegs are crucial in enabling the insect to become airborne.

MATERIALS AND METHODS

Seven species of treehoppers were collected on low vegetation in and around Halifax, NS, Canada, in August 2007 and in September and October 2010; *Campylenchia latipes* (Say) (10 animals, 31 videos of jumping captured), *Carynota marmorata* (Say) (1 animal and 10 jumps), *Ceresa basalis* Walker (5 animals and 20 jumps), *Entylia carinata* (Forster 1771) (12 animals and 60 jumps), *Publilia concava* (Say 1824) (10 animals and 57 jumps), *Telamona compacta* Ball [or *Telamona ampelopsidis* (Harris)] (1 animal and 12 jumps) and *Stictocephala bisonia* (= *Ceresa tauriniformis*) (Kopp and Yonke) (2 animals and 20 jumps). *Stictocephala bisonia* was also collected near Ljubljana, Slovenia, in August 2004. An eighth species, *Sextius* sp. (probably *S. virescens*) (4 animals and 36 jumps) was collected in Canberra, ACT, Australia, in February 2009. *Publilia*, *Entylia* and *Campylenchia* were locally common, but all the other species were found only occasionally. All belong to the family Membracidae (order Hemiptera, suborder Auchenorrhyncha, and superfamily Membracoidea). They were selected to show the range of body sizes and shapes in treehoppers from the sites studied.

Sequential images of jumps were captured at rates of 5000 s^{-1} and an exposure time of 0.05, 0.1 or 0.2 ms, with a single Photron Fastcam 512PCI camera [Photron (Europe) Ltd, West Wycombe, Bucks, UK], fitted with a 100 mm micro Tokina lens. Images were fed directly to a portable computer for later analysis. Jumps occurred spontaneously, or were encouraged by delicate mechanical

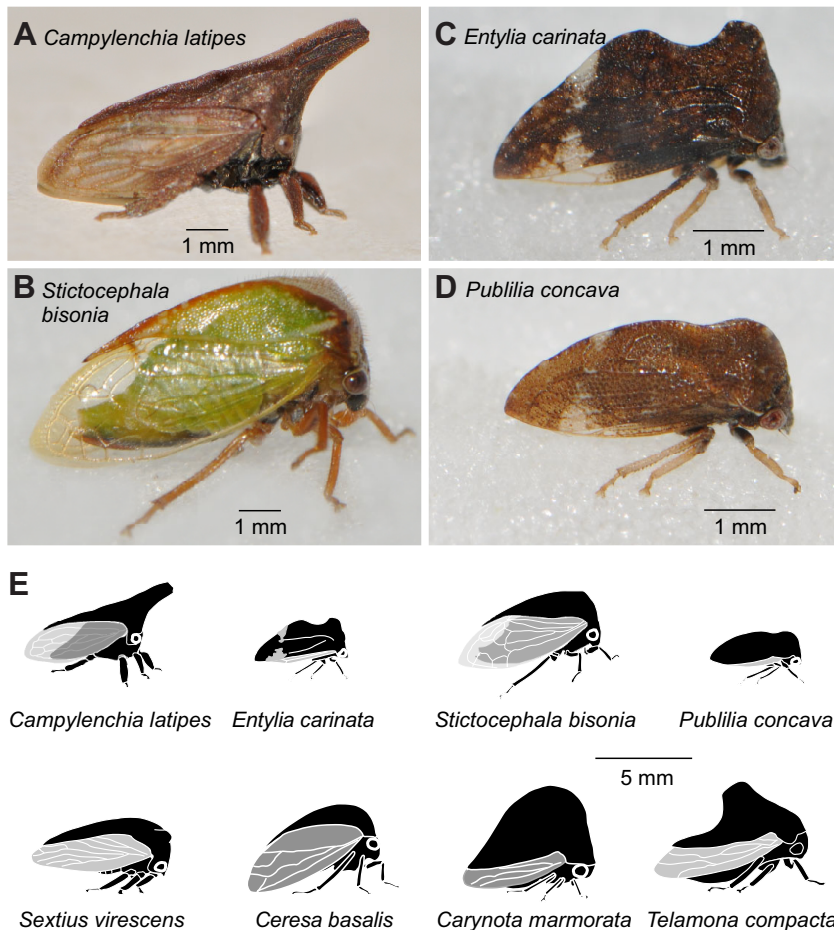


Fig. 1. Photographs of females of four species to show some of the diversity of body sizes and shapes of membracids analysed here: (A) *Campylenchia latipes*, (B) *Stictocephala bisonia*, (C) *Entylia carinata* and (D) *Publilia concava*. (E) Cartoons of all eight species studied here, drawn to the same scale. They all have a prominent posterior protrusion from the prothorax, and *Campylenchia* has an anterior one.

stimulation with a fine paintbrush, in an 80×80 mm chamber of optical quality glass, 10 mm deep at the bottom expanding to 25 mm at the top. The floor was made of high density foam to give an insect traction at take-off. The camera pointed directly at the middle of the front face of the chamber, the shape of which constrained most jumps into the image plane of the camera but other views of the body when jumping were also captured. Measurements of changes in joint angles and distances moved were made from jumps that were, as close as possible, parallel to the image plane of the camera. Jumps that deviated from this image plane by $\pm 30^\circ$ were calculated to result in a maximum error of 10% in the measurements of joint or body angles and distances. Body angle was defined as the angle subtended by the body's longitudinal axis relative to the horizontal. 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). Peak velocity achieved during take-off was calculated as the distance moved in a rolling 3-point average of successive images during the final millisecond before take-off. Measurements of these body movements were made from a point on the body close to the centre of mass (measured by balancing an insect on a pin) and just behind the origin of a hindleg, which could be recognised in all images taken from a side view. The time at which the hindlegs lost contact with the ground, so that the insect became airborne, was designated as time $t=0$ ms. This allowed different jumps to be aligned and compared. The time at which the hindlegs first moved 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 hindlegs and the take-off time would result in a 10% error in measuring acceleration time. All data are given as means \pm s.e.m. Temperature ranged from 24 to 30°C. Supplementary material Movies 1–3 show jumps captured at 5000 images s⁻¹ and replayed at 10 images s⁻¹.

The anatomy of the hindlegs and metathorax was examined in intact treehoppers, in those fixed and stored in 70% alcohol or 50% glycerol, and after they were cleared overnight in 5% potassium hydroxide. Drawings were made with the aid of a drawing tube attached to a Leica MZ16 stereo microscope (Wetzlar, Germany). Photographs were taken as colour (RGB) TIFF files with a Micropublisher 5.0 digital camera (Q-Imaging, Marlow, Bucks, UK) attached to the same microscope. Photographs of intact treehoppers were taken with a Nikon D90 camera fitted with a 100 mm Nikon macro lens. Lengths of the legs of fixed specimens were measured against a ruler to an accuracy of 0.1 mm from images captured with a digital camera attached to a Leica MZ16 microscope and projected onto a 24 in monitor. Body masses were determined to an accuracy of 0.1 mg with a Mettler Toledo AB104 balance (Beaumont Leys, Leics, UK).

RESULTS

Body shape

The body shape of the treehoppers analysed here (shown as photographs and cartoons in Fig. 1) was heavily influenced by the prothoracic helmet, which projected backwards and dorsally over the body in all species, but also prominently forwards in the rose thorn mimic *Campylenchia*. An occasional member of this species lacked the forward-pointing protrusion of the helmet, but the backward part was still present. The front of the head of most species was blunt and not streamlined as in leafhoppers. The eyes were placed toward the ventral margins of the head, facing laterally and forward.

These treehoppers analysed had an 11-fold range of body masses, 3.8–41 mg, and a 2-fold range of body lengths, 4.1–8.4 mm, with male *Publilia* being both the lightest and shortest, and *Telamona* being the heaviest and longest (Table 1). Across all species, body mass and length were correlated ($R^2=0.771$, $P=0.0004$).

Table 1. Body form of membracids

	Body mass (mg)	Body length (mm)	Hindleg length		Ratio of leg lengths			Hindleg length (% body length)	Hind leg length/ body mass ^{1/3} (mm mg ⁻¹)
			Femur (mm)	Tibia (mm)	Front	Middle	Hind		
<i>Publilia concava</i>									
Female (N=10)	4.5 \pm 0.4	4.7 \pm 0.1	0.8 \pm 0.03	1.6 \pm 0.1	1	1.1	1.6	86	1.8
Male (N=8)	3.8 \pm 0.3	4.1 \pm 0.03	0.8 \pm 0.1	1.4 \pm 0.1	1	1	1.5	88	1.9
<i>Entylia carinata</i>									
Female (N=7)	5.9 \pm 0.3	4.6 \pm 0.04	0.8 \pm 0.04	1.4 \pm 0.01	1	1	1.5	82	1.7
Male (N=7)	4.8 \pm 0.3	4.2 \pm 0.1	0.7 \pm 0.1	1.5 \pm 0.1	1	1.1	1.6	83	1.6
<i>Campylenchia latipes</i>									
Female (N=17)	10.3 \pm 0.4	7.8 \pm 0.1	0.8 \pm 0.04	1.6 \pm 0.04	1	1.2	1.4	47	1.5
Male (N=9)	6.6 \pm 0.2	5.6 \pm 0.1	0.7 \pm 0.1	1.5 \pm 0.04	1	1.1	1.3	58	1.7
<i>Sextius</i> sp. (N=4)	18.7 \pm 3.5	6.9	1.1	1.9	1	1.1	1.3	61	1.6
<i>Carynota marmorata</i> (N=1)	25	7.2	1.5	2.7	1	1.1	1.6	77	1.9
<i>Stictocephala bisonia</i> (N=4)	26.8 \pm 4.6	7.8 \pm 0.5	1.8 \pm 0.2	2.4 \pm 0.1	1	1	1.5	69	1.8
<i>Ceresa basalis</i> (N=5)	28.5 \pm 7.4	6.9 \pm 0.6	1.6 \pm 0.1	3.0 \pm 0.2	1	1.2	1.6	94	2.1
<i>Telamona compacta</i> (N=1)	41.2	8.4	1.1	1.9	1	1	1.4	70	1.7

Body length and mass, and lengths of the hindleg femora and tibiae in the eight species of membracids analysed. The ratio of leg lengths is given relative to the length of the front legs. N, the number of individuals from which the measurements were taken.

In *Entylia* and *Campylenchia*, for which there were larger data sets, the females were significantly heavier than the males; *Entylia*, 5.9 ± 0.3 mg compared with 4.8 ± 0.3 mg (independent samples two-tailed *t*-test, equal variance assumed unless otherwise stated, $t_{16}=3.2$, $P=0.006$); *Campylenchia*, 10.3 ± 0.4 mg compared with 6.6 ± 0.2 mg ($t_{22.04}=9.1$, $P<0.001$, equal variance not assumed here), for females and males, respectively. In *Publilia*, however, the females were not significantly heavier than the males (4.5 ± 0.4 mg compared with 3.8 ± 0.3 mg; two-tailed *t*-test, $t_{16}=1.6$, $P=0.124$).

Female *Publilia* were, nevertheless, significantly longer than the males (4.7 ± 0.1 mm compared with 4.1 ± 0.03 mm; two-tailed *t*-test, $t_{39.6}=8.4$, $P<0.001$, non-equal variance). The same relationship also held in *Entylia* (4.6 ± 0.04 mm compared with 4.2 ± 0.1 mm; two-tailed *t*-test, $t_{20.6}=5.8$, $P<0.001$, non-equal variance), and particularly in *Campylenchia*, where the females were much longer than the males (7.8 ± 0.1 mm compared with 5.6 ± 0.1 mm; two-tailed *t*-test, $t_{24}=21.5$, $P<0.001$), largely because of a longer forward projection of the helmet.

The length of the legs expressed relative to the length of the front legs ranged from 1:1.1:1.3 (front leg:middle leg:hindleg) in *Sextius* and male *Campylenchia*, to 1:1:1.6 in *Ceresa basalis*, *Carynota*, female *Publilia* and male *Entylia*. The hindlegs represented only 47% of overall body length in female *Campylenchia*, rising to 61% in *Sextius* and reaching 94% in *Ceresa*. The figure in *Campylenchia* is artificially low because of the extra length of the forward-pointing helmet. At most, therefore, the hindlegs were short, never more than 60% longer than the front legs and never longer than the body. The ratios of the length of the hindlegs relative to the cube root of the body mass ranged from 1.5 in female *Campylenchia* to 2.1 in *Ceresa* (Table 1).

In each species, the hindlegs were slung beneath the body and both moved in the same plane almost parallel with the undersurface of the body (Fig. 2). The hind coxae were large, extending from the anterior to the posterior edge of the metathorax and from the midline to the lateral edges (Fig. 2A). They were closely opposed to each other at the midline, but were not linked by press fastener-like structures ('poppers' or 'press studs') found in many leafhoppers (Burrows, 2007a; Emeljanov, 1987; Gorb, 2001). Both coxae were indented ventrally and laterally to accommodate the femora when the hindlegs were swung forwards and fully levated in preparation for jumping. A ventral hair plate in this indented region of a coxa would be stimulated by contact of the femur and potentially could signal that the hindleg was fully levated. When a coxa was viewed laterally, it could be seen to pivot with the lateral wall of the thorax (Fig. 2B), allowing a forward and backward rotation of about 20 deg. A prominent but small trochantin was visible laterally between the ventral and lateral wall of the thorax and the anterior edge of the coxa, but its actions in jumping are not known (Fig. 2). This arrangement of the coxae is similar to that in leafhoppers (Cicadellidae) but differs from that in froghoppers (Cercopidae) and planthoppers (Fulgoroidea). The trochanter was small and pivoted ventrally and dorsally with the coxa. This allowed movements through about 130 deg under the control of large trochanteral depressor muscles and smaller levator muscles in the thorax. By contrast, the joint between the trochanter and the femur allowed only a small angular excursion.

The increased length of a hindleg relative to the other legs resulted from a longer femur and tibia, with the tibia in larger species being slightly longer than the femur (Table 1). Both the femur and tibia have a significant correlation with the total leg length (in the five species with $N>3$ individuals each, the Pearson correlation coefficient for the femur against total leg length ranged from 0.698 to 0.995; for

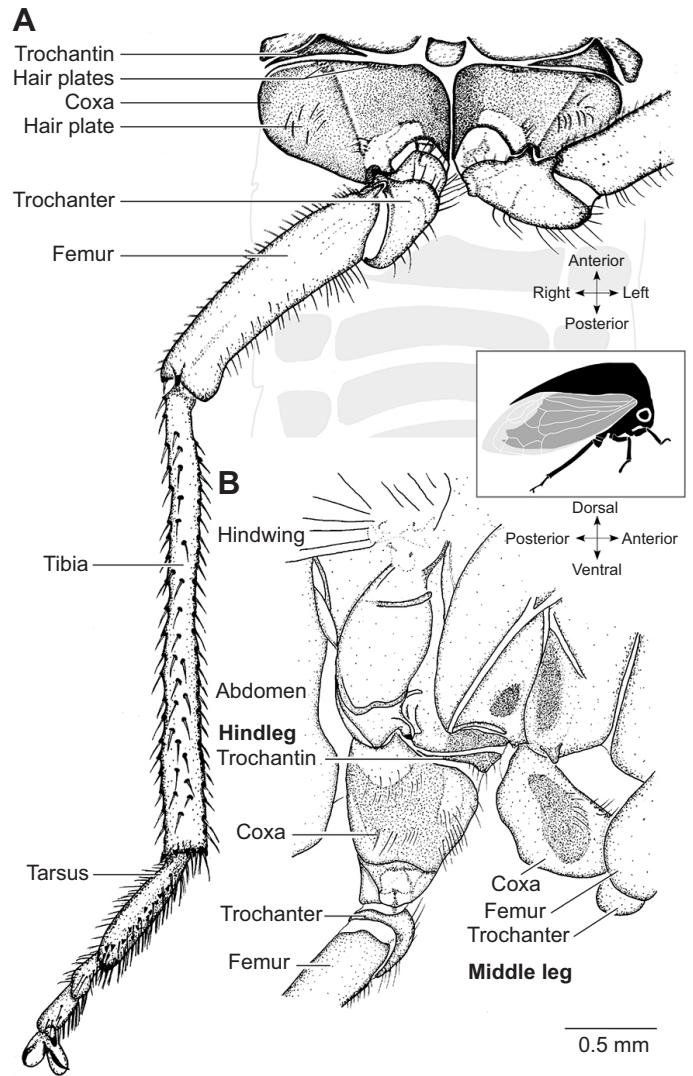


Fig. 2. Drawing of the hindlegs of a female *Stictocephala bisonia*, the shape of which is shown in the cartoon inset. (A) Ventral surface of the metathorax, hindlegs and abdomen. The right hindleg is shown depressed at the coxo-trochanteral joint and extended at the femoro-tibial joint. The left hindleg is shown in a partially levated position and is truncated in the middle of the femur. The anterior abdominal segments are shown in grey. (B) Side view of the right side of the thorax showing the articulations of the coxae of the right hindleg and right middle leg.

the tibia, this was 0.499 to 0.982), suggesting that both segments make a strong contribution to the overall length of the hindlegs.

The hairs on the tibia were stouter than those on the femur but they did not form prominent rows as found in cicadellids. At the joint with the tarsus, a semi-circle of short and thin hairs was present that did not appear to be capable of improving friction with the substrate during jumping. This is in contrast to the stout ventrally pointing spines in this position that characterise many other auchenorrhynchan bugs including cicadellids. The three main segments of the tarsi had numerous hairs and two hooks on the most distal part.

Kinematics of the jump

Jumping movements of treehoppers were analysed from high speed videos taken from different camera angles (Figs 3, 4; supplementary

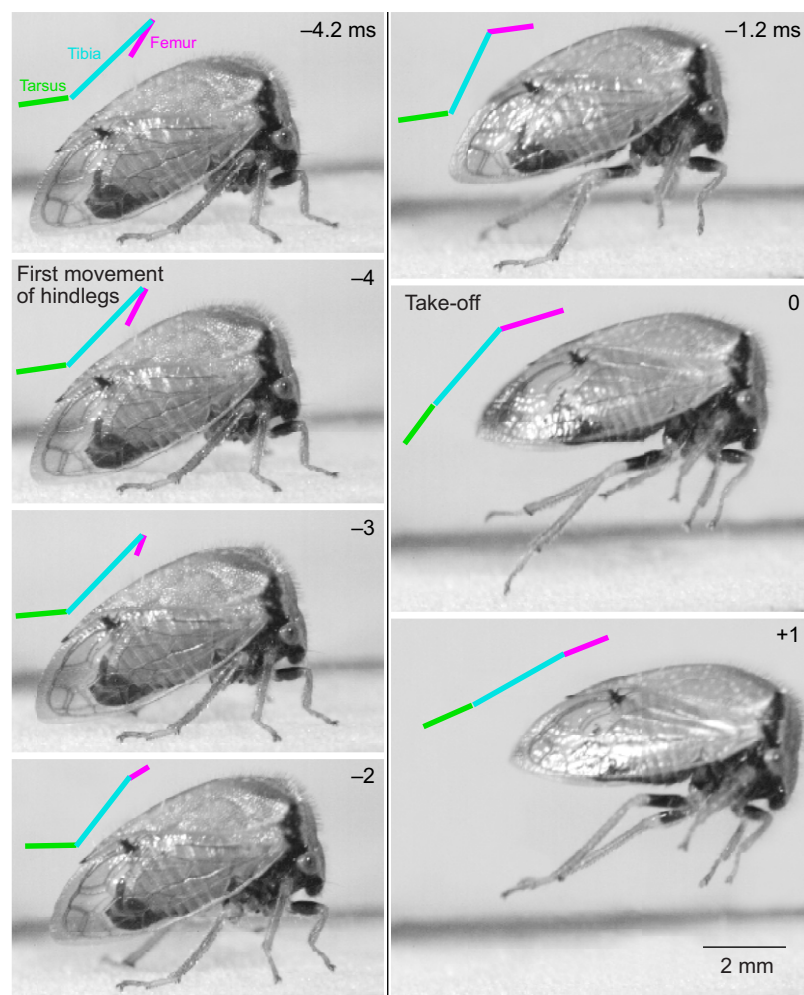


Fig. 3. Side view of *Ceresa basalis* jumping from a horizontal surface, captured at $5000 \text{ images s}^{-1}$ and with an exposure time of 0.05 ms . In this and Figs 4 and 6–8, the following conventions are used: selected images are arranged in two columns at the times indicated, with take-off designated as $t=0 \text{ ms}$; the bottom left-hand corner of each image represents a constant point of reference. In addition, the positions of the different segments of the right hindleg are indicated by colour-coded lines: femur in pink, tibia in cyan and tarsus in green.

material Movies 1–3). Side views of a treehopper as it jumped from the horizontal floor provided detailed information about the timing of movements by the different legs, in particular the first movements of the hindlegs and the time at which they lost contact with the ground (Fig. 3, Fig. 5A). These allowed acceleration times, body angle at take-off, and trajectories at and after take-off to be determined. Alternative views from underneath as a treehopper jumped from the vertical glass surface of the chamber gave detailed information about the sequence of movements of individual joints and of the co-ordination between the two hindlegs (Fig. 4, Fig. 5B).

The first movement of the hindlegs in preparation for jumping was a levation movement of the coxo-trochanteral joints. The effect was to rotate both hindlegs forwards so that the femora were pressed into the ventral indentations of the coxae. The tibiae were also flexed about the femora and the tarsi were placed on the ground at the lateral edges of the abdomen and directly beneath the edges of the wings (Fig. 4; supplementary material Movie 1). These positions were then held for variable periods that could extend to seconds, but there was always a minimum period of a few hundred milliseconds before a jump was generated. Adjustments of the front and middle legs set the angle of the body relative to the substrate. This angle was low even at take-off, ranging from 4° in male *Entylia* to 18° in *Carynota*, with notable exceptions being both male and female *Campylenchia* in which the body angle was 40 – 41° (Table 2). This means that for most treehoppers the body was at a shallow angle to the ground at take-off.

This preparatory period was then followed by a rapid and simultaneous depression and extension of both hindlegs and forward propulsion of the body to take-off in a jump. The first visible movement of a hindleg was a depression movement of the coxo-trochanteral joint, most clearly seen in views from underneath (Fig. 4). In side views where the trochanter was largely obscured, this initial movement was manifested as a downward and backwards movement of the femur that was closely linked to the trochanter, which resulted in the whole tarsus being pressed firmly against the substrate. The continuing depression of the hindleg trochanter caused a further downward movement of the femoro-tibial joint (Fig. 3, Fig. 5A) and was accompanied by extension of the tibia (Figs 3, 4). These movements propelled the body forwards and raised it from the ground so that first the middle legs and then the front legs lost contact with the ground. In the last stages of a jump, therefore, only the hindlegs were in contact with the ground and could provide propulsion. Throughout the acceleration phase of a jump, the velocity of the forward movement of the body continued to rise and reached a peak at take-off, declining once all legs had lost contact with the ground and the insect was airborne (Fig. 5A). The initial joint movements of the two hindlegs occurred simultaneously within a time resolution of 0.2 ms set by the frame rate of 5000 s^{-1} used to capture the jumps (Fig. 5B). In a few jumps, one trochanter was seen to move 0.2 ms (1 frame) before the other, but no greater asynchronies were seen. Both the coxo-trochanteral and femoro-tibial joints reached the full extent of their movements at take-off

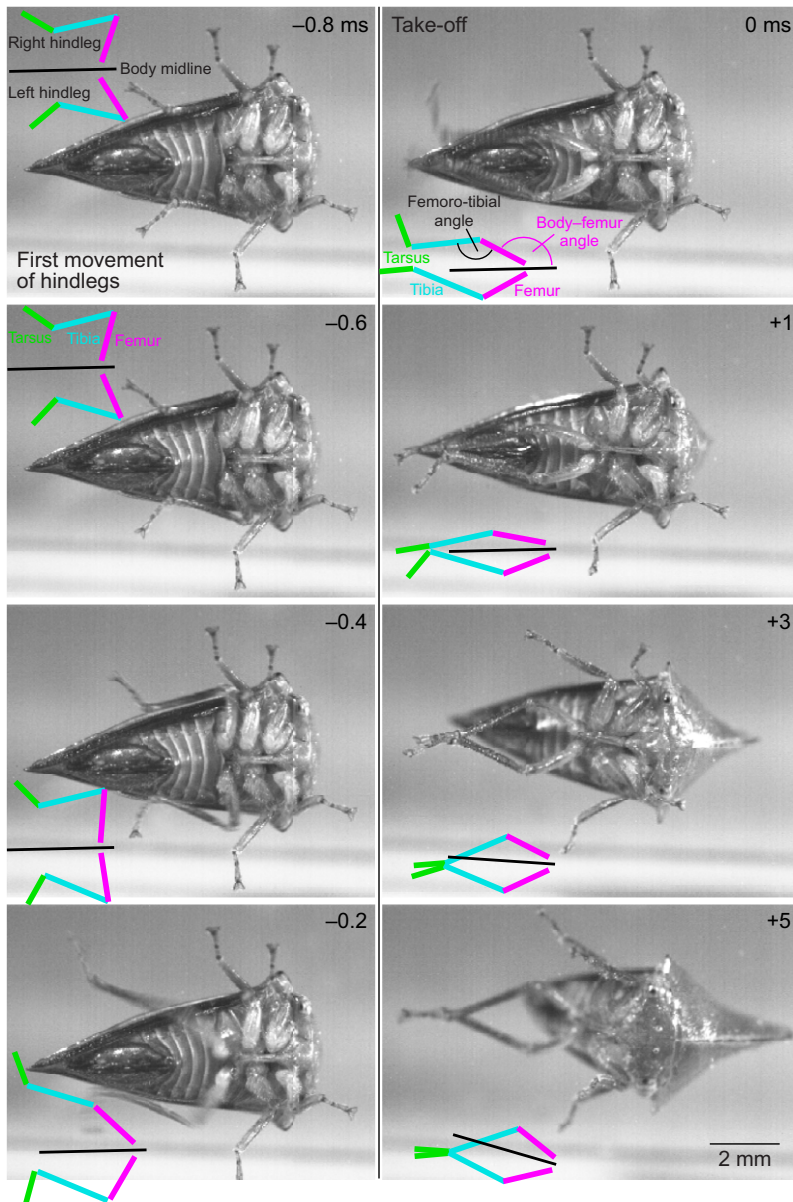


Fig. 4. Ventral view of *Carynota marmorata* jumping from the front glass wall of the chamber captured at 5000 images s^{-1} and with an exposure time of 0.05 ms. The hindlegs slipped so that the total acceleration time was short and the body pitched forwards after take-off. The positions of the different segments of the right and left hindlegs are indicated by the colour-coded lines as in Fig. 3, with the midline body axis in black. A video of this jump is shown in supplementary material Movie 1.

(Fig. 4, Fig. 5B). At, or just after take-off, both hindleg tarsi came together at the midline of the body and in some jumps then crossed. The hindlegs remained fully depressed and extended during the initial airborne trajectory of a jump.

The same sequence and pattern of leg movements was seen in all species analysed. For example, in *Telamona* (Fig. 6; supplementary material Movie 2) and *Campylenchia* (Fig. 7), depression of the hindleg trochanters was the first movement of the hindlegs and was accompanied by extension of the hindleg tibiae. The front and middle legs of both species lost contact with the ground before take-off so that only the hindlegs propelled the body in the final stages of the jump.

Jumping and wing movements

In all of the jumps just described, the wings remained folded and thus could not have been contributed to the performance. Sometimes, however, the wings were opened and flapped before take-off so that a smooth transition to flapping flight was achieved (Figs 8, 9; supplementary material Movie 3). The point of take-off when the

hindlegs lost contact with the ground occurred at different times relative to the elevation and depression phases of the wing beat cycle. In the example shown, take-off occurred during the depression of the wing beat cycle (Figs 8, 9), but in different jumps by different species it could occur later in this phase or during elevation. At other times, the wings were opened a few hundred milliseconds before take-off, then held stationary in an elevated position, before being moved only as the hindlegs propelled take-off. A further variant of the behaviour was that the wings were opened and then flapped for a variable number of cycles before take-off; in this behaviour, the crucial role of the hindlegs in propelling take-off could still be demonstrated (Fig. 9). In this jump, the wings were first elevated about 180 ms before take-off and were then flapped rhythmically for a few cycles, but with elevations and depressions of less than their full excursion (Fig. 9A). The legs remained on the ground and only small movements of the body were associated with each wing beat. There was then a pause during which the wings remained partially elevated but were not moved. About 40 ms before take-off, the wings were elevated further and were then flapped at

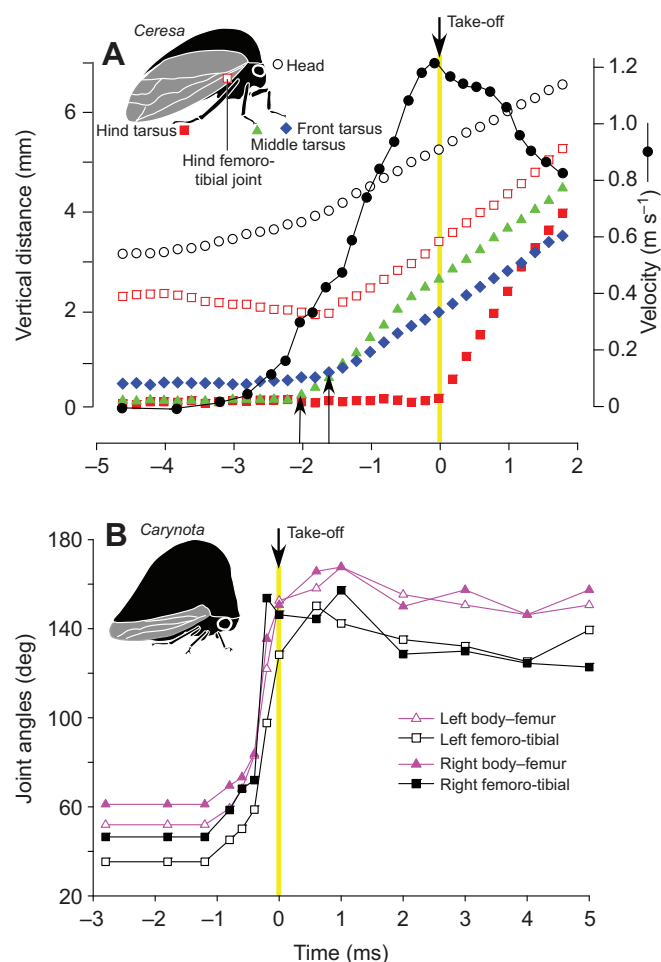


Fig. 5. Graphs of the movements of the hindlegs during jumping. (A) *Ceresa basalis* viewed from the side (see Fig. 3). The positions of the tarsi of the three right legs, the femoro-tibial joint of the right hindleg and the head are plotted during a jump. The instantaneous forward velocity of the body is also plotted (linked black circles). The black upward arrows indicate the time when the middle and front legs lost contact with the ground. Take-off occurs at time 0 ms and is indicated by the vertical yellow bar. (B) *Carynota marmorata* viewed from underneath (see Fig. 4). The changes in the angle of the femur relative to the body, and the femoro-tibial angle (as indicated in Fig. 4) of the right and left hindlegs are plotted against time.

full amplitude for six cycles (Fig. 9B). The first five cycles of wing beats produced barely detectable upward movements of the body, but on the sixth cycle the hindlegs were suddenly depressed and extended in a jump that then lifted the body from the ground. These observations indicate that the hindlegs propel take-off and that the wing movements on their own may not generate sufficient lift to enable the insect to become airborne.

Do wing movements assist the heavier species of treehopper to become airborne? If this were true then there should be a correlation between the use of wings for jumping and body mass. *Stictocephala*, one of the heaviest treehoppers, had the most jumps accompanied by wing movements (57%), but a slightly heavier species, *Ceresa*, had only 31% of its jumps in this category, whereas the lightest species, *Publilia*, had 39% (Fig. 10). Across the different species of treehoppers, the percentage of jumps that were accompanied by wing movements was not related to body mass.

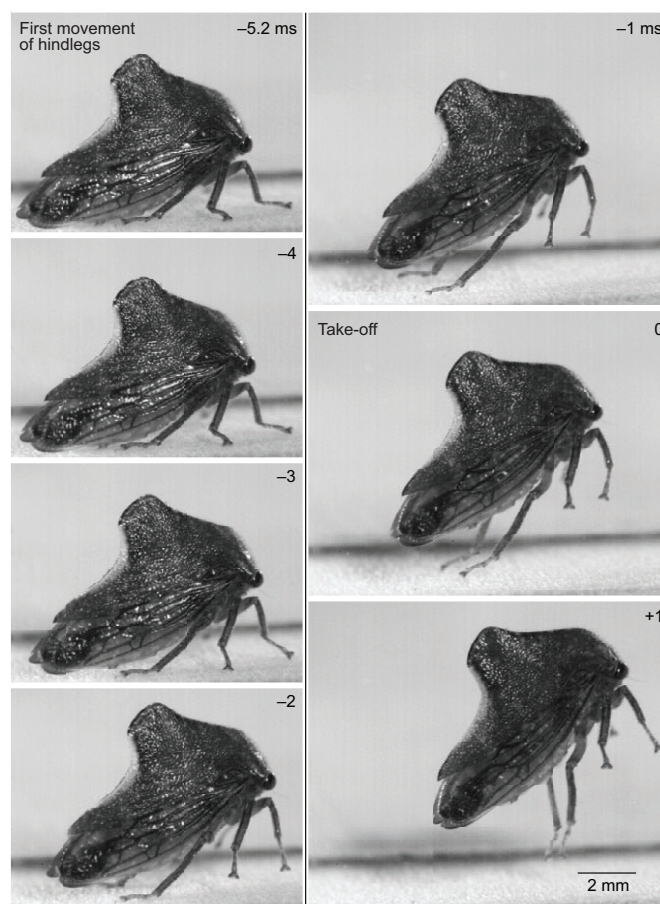


Fig. 6. Jump of *Telamona compacta* from a horizontal surface and viewed from the side, captured at 5000 images s^{-1} and with an exposure time of 0.05 ms. Take-off was achieved in 5.2 ms. A video of this jump is shown in supplementary material Movie 2.

Jumping trajectories

Trajectories were determined by plotting the position of the approximate centre of mass of the body (just posterior to the hindlegs) against time, as measured from sequential frames of the high speed videos. The mean angle of the trajectory of a jump varied only over a narrow range across all the species, from 47 deg in male *Entylia* to 64 deg in *Telamona* (Table 2). The variation within different jumps by the same species was also small and there were no significant differences in the trajectories of males and females of a particular species. Once airborne, the body did not spin rapidly about any of the three body axes, but most trajectories could only be followed for the first few milliseconds after take-off and none could be followed to a natural landing. A possible use of the wings could be to stabilise the trajectory of a jump against rotation.

Jumping performance

These kinematic analyses allowed jumping performance to be defined. Take-off velocity was measured as a rolling three-point average from successive frames (at 0.2 ms intervals) just before take-off. In the best jumps, velocity ranged from 2.0 m s^{-1} in *Ceresa* to 2.7 m s^{-1} in *Entylia* (Table 2). Acceleration times varied widely between different species; in the lighter species it was short at 1.2–1.3 ms, but in some of the heavier species it was about three times as long at 3.5–3.7 ms. Body mass was correlated with

Table 2. Jumping performance of membracids

	Body mass (mg)	Time to take-off (ms)	Take-off velocity (m s ⁻¹)	Take-off angle (deg)	Body angle at take-off (deg)	Acceleration (m s ⁻²)	g-force (g)	Energy (μJ)	Power (mW)	Force (mN)
Formula/symbol	<i>m</i>		<i>v</i>			<i>f=v/t</i>	<i>g=f/9.81</i>	<i>e=0.5mv²</i>	<i>Power=e/t</i>	<i>Force=mv</i>
<i>Publilia concava</i>										
Female (N=4, n=21)	4.5±0.4	1.2±0.1	1.8±0.2	61±6	9±4	1500	153	7	6	7
Male (N=4, n=25)	3.8±0.3	1.3±0.04	2.2±0.3	63±4	12±3	1690	173	9	7	6
Best	4	1.1	2.6	44	12	2360	241	13	12	10
<i>Entylia carinata</i>										
Female (N=6, n=34)	5.9±0.3	1.2±0.04	2.1±0.4	49±7	9±2	1750	178	13	11	10
Male (N=3, n=16)	4.8±0.3	1.2±0.03	2.5±0.1	47±1	4±1	2080	212	15	12	10
Best	5.3	1.1	2.7	44	3	2450	250	19	18	13
<i>Campylenchia latipes</i>										
Female (N=5, n=12)	10.3±0.3	1.3±0.1	1.6±0.1	54±9	40±11	1230	126	13	10	13
Male (N=3, n=9)	6.6±0.2	1.3±0.1	1.7±0.04		41±1	1310	133	9	7	9
Best	7	1.2	2.3	73	38	1670	170	14	12	12
<i>Sextius</i> sp.										
Mean (N=4, n=29)	18.7±3.5	1.9±0.1	1.8±0.2	54±8	7±3	950	97	30	16	18
Best	24	1.8	2.1	61	4	1220	125	58	32	29
<i>Carynota marmorata</i>										
Mean (N=1, n=7)	25	2.8±0.2	2.2±0.2	58±2	18±2	780	80	60	22	20
Best	25	2.5	2.5	82	16	960	98	78	30	24
<i>Stictocephala bisonia</i>										
Mean (N=2, n=14)	26.8±4.6	3.6±0.1	2.1 ±0.2	51±4	16±1	580	59	59	16	16
Best	28	3.5	2.7	54	15	770	79	101	29	21
<i>Ceresa basalis</i>										
Mean (N=5, n=13)	28.5±7.4	3.5±0.1	1.6±0.4	48±5	12±1	460	47	36	10	13
Best	33	3.4	2	52	10	590	60	66	19	19
<i>Telamona compacta</i>										
Mean (N=1, n=9)	41	3.7±0.2	1.4±0.2	64±2	26±1	380	39	40	11	16
Best	41	3.4	1.9	62	24	560	47	74	22	23

The jumping performance of the eight species of membracids analysed. The data are the mean of means ± s.e.m. for the performance of individuals except for *Carynota* and *Telamona* where they are the means of all jumps by a single individual. The values in the five columns on the right were calculated from the mean values given in the four columns on the left.

The best performance of a particular individual for each species is also given. Only data for the jumps that were viewed from the side are presented here. N, the number of insects analysed in this table; n, the number of jumps.

acceleration time ($R^2=0.905$, $P<0.0001$) across the different species (Fig. 11A). Hindleg length was also correlated with acceleration time ($R^2=0.922$, $P<0.0001$) (Fig. 11B); it takes more time to accelerate a longer leg. By contrast, neither body mass nor acceleration time was correlated with take-off velocity (Fig. 11C,D). In the best jumps, the applied accelerations ranged from 560 to 2450 m s⁻² across the different species, with the lower values in the heavier species and the higher values in the lighter ones (Table 2). Similarly, the energy required to achieve this performance ranged from 13 to 101 μJ, with the lower values this time in the lighter species and the higher ones in the heavier species (Table 2). The power output ranged from 12 to 32 mW, depending on the acceleration time during which energy was expended. The force exerted during the best jumps was at its lowest at 10 mN in the lightest species and at its highest at 29 mN in one of the heavier species. No reliable measurements of distances jumped could be made because it was not possible to follow the complete trajectories of jumps and therefore distinguish those powered solely by the hindlegs from those that were assisted by flapping flight.

DISCUSSION

Jumping in treehoppers is powered by rapid depression of the hind trochantera. The first visible movements of the hindlegs were depression of the trochantera followed by extension of the tibiae. These movements accelerated the body to mean take-off velocities of 2.1–2.7 m s⁻¹ in mean times of 1.2 ms in the lighter treehoppers

and in 3.7 ms in the heavier ones, so that in its best jump a treehopper experienced a force of up to 250 g. The front and middle legs lost contact with the ground before take-off and, even when the wings were flapped, it was the propulsive movements of the hindlegs that enabled a treehopper to become airborne. The power output per mass of muscle ranged from 5300 to 33,000 W kg⁻¹ in the best jumps of the different species analysed. Assuming that the mass of the jumping muscles (hind trochanteral depressors) represented about 11% of body mass [as in froghoppers (Burrows, 2006a) and locusts (Bennet-Clark, 1975)], these values therefore far exceed the maximum active contractile limit of normal muscle. Direct contraction of the muscles would only produce power outputs from 250 to 500 W kg⁻¹ (Askew and Marsh, 2002; Ellington, 1985; Josephson, 1993; Weis-Fogh and Alexander, 1977). The conclusion is that jumping must be propelled by a catapult mechanism, as in the closely related leafhoppers (Burrows, 2007b), and in froghoppers (Burrows, 2006a), planthoppers (Burrows, 2009a) and other insects such as fleas (Bennet-Clark and Lucey, 1967) and locusts (Bennet-Clark, 1975; Heitler and Burrows, 1977).

Design for jumping

The overall body shape of treehoppers does not appear to be primarily adapted for speed of jumping. The head of many species can be broad and blunt without any of the streamlining seen in leafhoppers and froghoppers. Furthermore, elaborations of the prothoracic helmet often lead to forward projections, as in

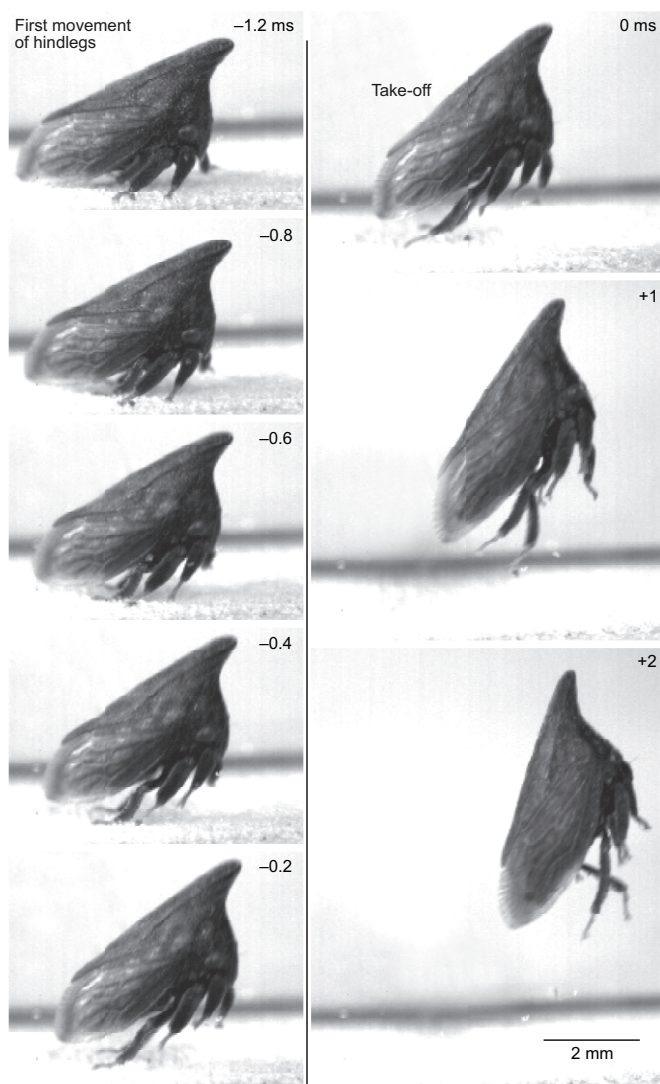


Fig. 7. Jump of a male *Campylenchia latipes* viewed from the side and captured at 5000 images s^{-1} with an exposure time of 0.05 ms. Take-off was achieved in 1.2 ms with a trajectory of 66 deg.

Campylenchia, or to prominent dorsal projections, as in *Carynota* or *Telamona*, that might be expected to increase wind resistance and thus reduce take-off velocity and curtail distance or height achieved. All would seemingly reduce the effectiveness of jumping as a means of escape from predators or as a launch into flight. Finally, some of these treehoppers are amongst the heaviest members of the Auchenorrhyncha that jump but there was no correlation between body mass and the frequency of use of wing movements before take-off. Even when the wings were flapped for several cycles whilst still on the ground, rapid depression of the hindlegs was necessary to launch a take-off. The importance of jumping in treehoppers can be gauged anatomically by the size of the jumping muscles and the space afforded to them in the thorax, and behaviourally from the readiness with which these insects will jump when placed in threatening circumstances.

The overall length of the hindlegs in treehoppers is short relative to both the length of the other legs (never more than 60% longer) and the length of the body (never more than 94%). By contrast, most cicadellid leafhoppers have hindlegs that are 200% longer than

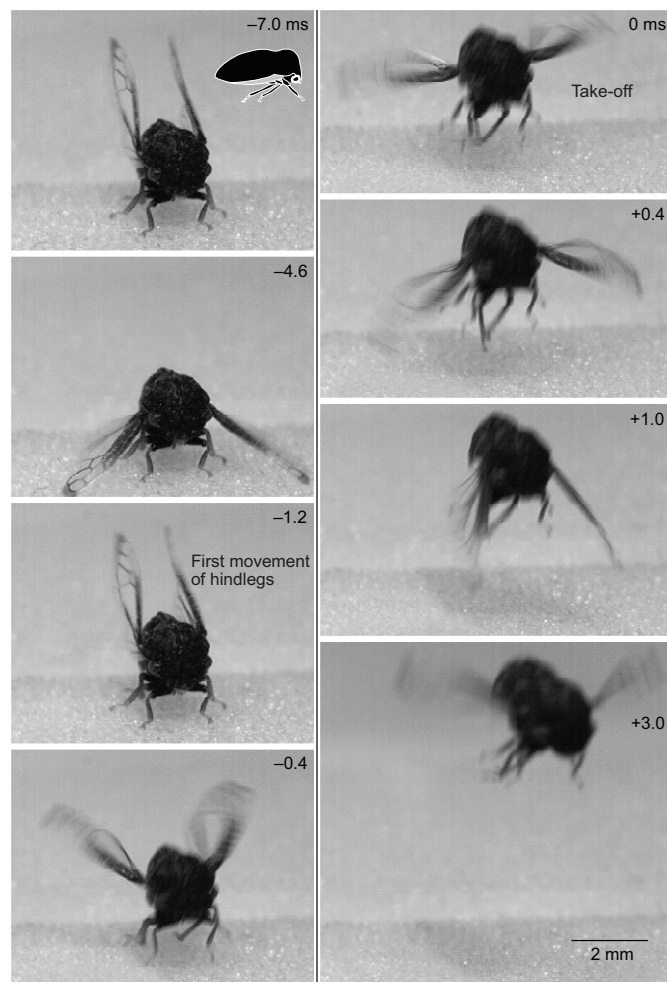


Fig. 8. Jump by a male *Publilia concava* viewed from in front and captured at 5000 images s^{-1} with an exposure time of 0.2 ms. Take-off occurred in 1.2 ms from the first movement of the hindlegs. The wings opened before the hindlegs started to move and were moving downwards at take-off. A video of this jump is shown in supplementary material Movie 3.

the front legs and 84% of the body length (Burrows, 2007a; Burrows, 2007b), but in the sister family Ulopinae (previously a sub-family of the cicadellids) the hindlegs are short (only 40% longer than the front legs and 58% of body length) (Burrows and Sutton, 2008). The comparable figures for froghoppers are that the hindlegs are 50% longer than the front legs and 65% the length of the body (Burrows, 2006a); in planthoppers the figures are 30% and 79%, respectively (Burrows, 2009a).

In the eight species analysed, both body mass and the length of the hindlegs correlated with the time that it took to accelerate to take-off. The larger the body size, the longer the legs, while their proportions relative to the other legs and to the length of the body were similar. It would take longer to accelerate a larger body mass and to extend long hindlegs. However, neither body mass nor length of the hindlegs correlated with take-off velocity. This supports the finding that the energy requirements of a jump must be met by a catapult mechanism because they far exceed those that could be generated by direct muscle action. In jumps propelled by a catapult mechanism, the length of the propulsive legs is of importance only in the time taken to deliver the energy stored by the catapult and thus the ground reaction forces that result (Burrows and Sutton,

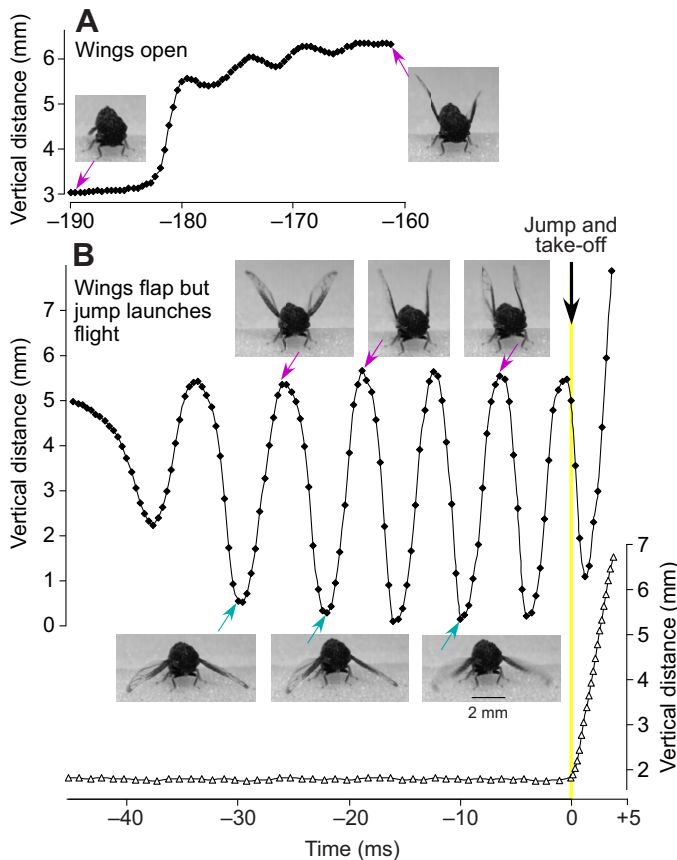


Fig. 9. Hindleg and wing movements of *Pubillia concava* during the jump shown in Fig. 8. (A) Plot of the height of the tip of the right front wing above ground against time before take-off. The wings opened about 185 ms before take-off and were moved rhythmically for a few cycles, but not over their full range. (B) A continuation of the same plot (filled diamonds) closer to take-off and with the height of the right eye above ground (open triangles) also plotted to represent the position of the body. The wings are now elevated and depressed through their full range at a frequency of 160 Hz. Only when the hindlegs depressed and extended fully did the insect become airborne.

2008). It would be advantageous to exert less ground reaction force on a flimsy substrate, suggesting a divergence between the leafhoppers and treehoppers based on the resilience of the plants they favour.

Jumping mechanisms

Jumping in treehoppers shows clear differences from the mechanisms described in leafhoppers, froghoppers and planthoppers, although all are powered by contractions of muscles in the thorax that move the hind trochanters. The structure of the proximal joints of the hindlegs most closely resembles that of leafhoppers, which are likely to be their closest relatives. The hind coxae in both are large so that they occupy most of the metathorax. Although they are closely opposed to each other at the midline, they are not linked, as are the hind coxae of many leafhoppers, by a protrusion from one that inserts in a depression in the medial surface of the other (Burrows, 2007a; Emeljanov, 1987; Gorb, 2001). Even without these coxal links, treehoppers can jump faster than most leafhoppers and this raises the question of what function they serve in leafhoppers and why they are not needed in treehoppers. By contrast, the hind coxae of froghoppers are smaller and the ventral surfaces of those

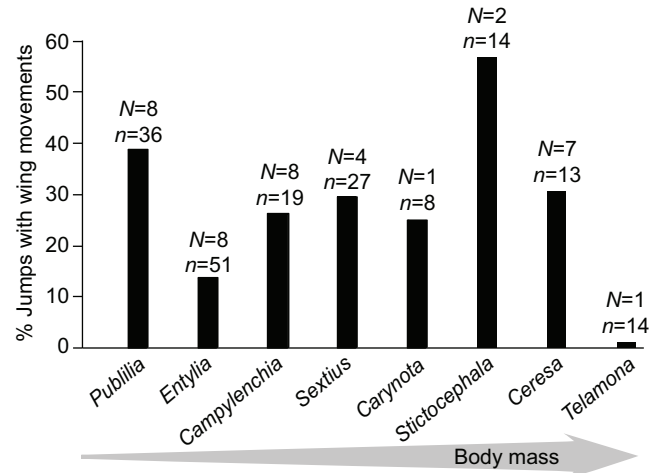


Fig. 10. Percentage of jumps accompanied by wing movements in eight species of treehopper. The species are arranged from left to right in order of their body mass. *N*, the number of animals of a particular species; *n*, the total number of jumps by that species included in the analysis.

in planthoppers are membranous and transparent. Froghoppers have a protrusion from a coxa covered in microtrichia that engages with a similarly covered protrusion of the femur when a hindleg is levated and cocked in preparation for a jump (Burrows, 2006b). These structures act as a constraint on depression while the depressor muscle contracts slowly to build up the energy necessary for a jump. In planthoppers, the coxal protrusion is still covered by microtrichia but the femoral protrusion is reduced to a flat, smooth plate guarded by hairs that may have a proprioceptive function (Burrows, 2009a). In leafhoppers, both the coxal and femoral protrusions are absent (Burrows, 2007a), a feature that is also found in treehoppers. It is not known how the hindlegs of tree and leafhoppers are held in place so that they do not move during the prolonged contraction of the trochanteral depressor muscles to store energy.

Jumping distance

It was not possible to determine by direct observation the height and distance achieved by treehopper jumps. A camera position (or particular lens) that resolved the movements of the individual legs was not able to record the full trajectory of a jump and one that could failed to show whether flapping movements of the wings also occurred much after take-off. Calculations based on standard equations for the motion of an inert body (Alexander, 1968) (Eqns 1 and 2 below) estimated the horizontal distance and vertical height achieved in a jump that did not involve wing movements, and assuming there was no aerodynamic drag on the body:

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

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

where *s* is the distance jumped, *h* is the maximum height reached, *v* is the instantaneous velocity at take-off, θ is the take-off angle (Table 2) and *g* is the acceleration due to gravity (9.81 ms^{-2}). On the basis of the values measured here, male *Entyllia* should generate the biggest jumps, achieving a horizontal distance of 740 mm (176 times its body length) and a vertical height of 200 mm (47 times body length). *Ceresa* would be the least able, achieving a distance of 405 mm (59 times body length) and a height of 112 mm (16 times body length). Across all the membracids analysed, predicted

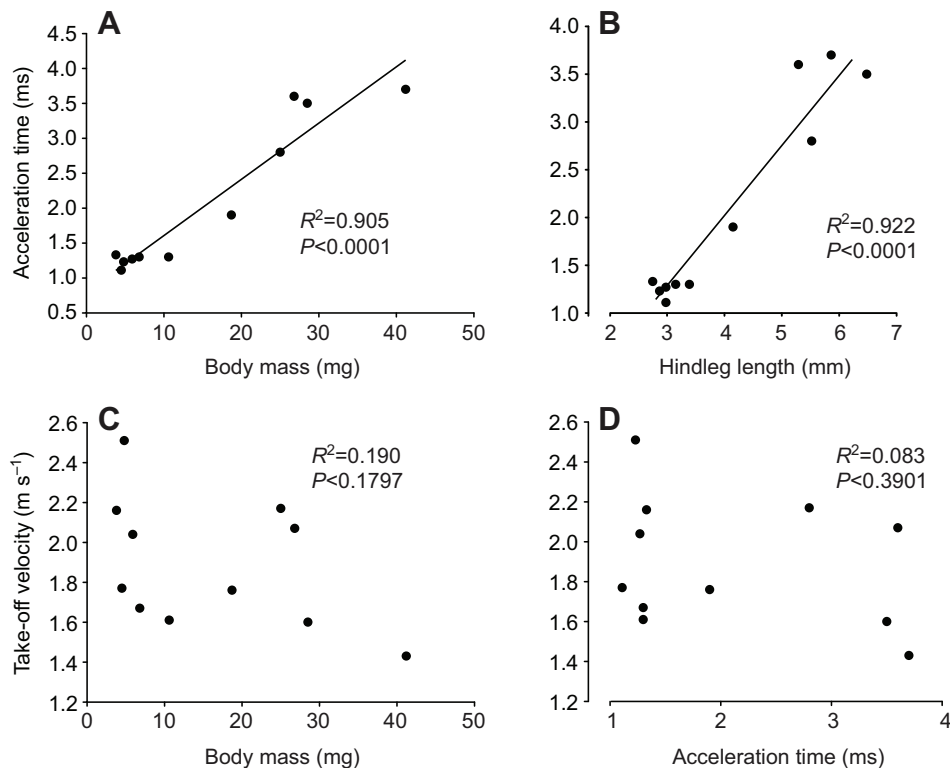


Fig. 11. Jumping performance as a function of body mass in the eight species of treehoppers studied here. (A) Acceleration time increased with increasing body mass. (B) Hindleg length was correlated with acceleration time. (C) Take-off velocity was not correlated with body mass. (D) Acceleration time and take-off velocity were not correlated. Data from males and females of *Entylia carinata*, *Publilia concava* and *Campylenchia latipes* are plotted separately; for the other species, data from the two sexes are lumped together.

performance did not correlate with body mass; *Carynota*, one of the heavier treehoppers, is predicted to achieve similar distances to those of *Publilia*, the lightest species analysed. None of these calculations include a contribution from wing movements, and they take no account of the wind resistance that is likely to be offered in inverse proportion to body size when moving at such high velocities (Bennet-Clark and Alder, 1979). Vogel has estimated that the froghopper *Philaenus*, which is about the same size as *Campylenchia*, would lose some 25% of its jumping range because of drag and that insects of a comparable size to the smaller treehopper species would lose even more (Vogel, 2005).

Jumping performance

Where does the jumping performance place treehoppers among other hemipterans and amongst other insects that power jump by movements of the legs? The shortest acceleration times occur in planthoppers and froghoppers, with take-off being achieved in about 0.8 ms in *Issus* and *Philaenus*. The smallest treehoppers take longer, 1.2 ms, comparable to the time taken by fleas (Sutton and Burrows, 2011) and short-legged leafhoppers (Burrows and Sutton, 2008), but shorter than the 2 ms taken by *Hackeriella* (Coleorrhyncha) (Burrows et al., 2007) and pygmy mole crickets (Burrows and Picker, 2010). Heavier treehoppers take correspondingly longer so that their acceleration times of 2–3.7 ms overlap with those of some long-legged leafhoppers (2.75–6.4 ms). These acceleration times are similar to the 4.4–6.4 ms taken by the shore bug *Saldula* (Hemiptera, Heteroptera) or the 6.6 ms taken by the snow flea *Boreus* (Mecoptera, Boreidae) (Burrows, 2011).

The take-off velocities of treehoppers (range 2–2.7 m s⁻¹) are higher than those of snow fleas at 0.8 m s⁻¹, *Hackeriella* (Coleorrhyncha) at 1.5 m s⁻¹ (Burrows et al., 2007), fleas at 1.9 m s⁻¹ (Bennet-Clark and Lucey, 1967; Sutton and Burrows, 2011), shore bugs *Saldula* at 1.8 m s⁻¹, and most leafhoppers except *Aphrodes*, which achieves velocities of 2.9 m s⁻¹ (Burrows, 2007b). The best

take-off velocities of treehoppers are comparable to those achieved by the fastest flea beetles: 2.7 m s⁻¹ in *Longitarsus gracilis* (Coleoptera, Alticinae) (Brackenbury and Wang, 1995) and 2.1 m s⁻¹ in the bush cricket *Pholidoptera griseoaptera* (Orthoptera, Ensifera, Tettigoniidae) (Burrows and Morris, 2003), and the false stick insect *Prosarthria teretirostris* (Orthoptera, Caelifera, Proscopiidae), with a take-off velocity of 2.5 m s⁻¹ (Burrows and Wolf, 2002). Treehoppers are, however, outperformed by desert locusts, which reach velocities of 3.2 m s⁻¹ (Bennet-Clark, 1975), the froghopper *Philaenus* at 4.7 m s⁻¹, and pygmy mole crickets and the planthopper *Issus*, both at 5.4 m s⁻¹.

On the basis of the distance and height jumped relative to body length, *Entylia* is calculated to generate the biggest jumps amongst membracids, achieving a calculated horizontal distance of 740 mm (176 times its body length) and a vertical height of 200 mm (47 times body length). These values match the best achievements of froghoppers, fleas, leafhoppers and planthoppers, which can all jump distances more than 100 times their body length. In its best jumps the long-legged leafhopper *Aphrodes* is calculated to achieve a distance of 825 mm (97 times body length) and height of 156 mm (18 times body length) (Burrows, 2007b), and the short-legged leafhopper *Ulopa* a distance of 496 mm (160 times body length) and a height of 187 mm (60 times body length) (Burrows and Sutton, 2008). The planthopper *Issus* was observed to jump a distance of 1100 mm (167 times body length) (Burrows, 2009a).

Jumping stability

Once airborne, the jumps of treehoppers were stable and initially the body did not rotate rapidly around any of its three axes. In this respect, their stability is similar to that of other auchenorrhynchan bugs but is in contrast to the jumps of pygmy mole crickets, which rotate in the pitch plane at rates of 100–190 Hz (Burrows and Picker, 2010), and Psyllids (Hemiptera, Sternorrhyncha, Psyllidae), which rotate at more than 300 Hz (Burrows, 2012). This stability means

that less energy is dissipated in rotation and increases the probability of a stable landing but at the expense of unpredictability that is introduced by rotation and which may aid in predator avoidance.

Despite possessing a variety of enlarged and seemingly unwieldy helmets, these treehoppers routinely achieved respectably large jumps that were also stable. This suggests that the shields in the species examined here may not be as aerodynamically unsophisticated as they first appear, but investigation would require direct aerodynamic tests. It remains to be determined whether this also extends to the South American species with elaborate knobs on their helmets (Prud'homme et al., 2011), or whether those particular examples even jump. At some point, the importance of token head ornaments in sexual selection, or some other selective advantage, presumably may prevail over aerodynamic utility in facilitating jump performance.

Future experiments

The implication that treehoppers use a catapult mechanism to jump poses a number of questions that will need to be addressed in future experiments. First, on what structural basis are the muscles able to generate the necessary force? The expectation would be that, as has been demonstrated in froghoppers, leafhoppers and planthoppers (Burrows, 2007a; Burrows, 2007c; Burrows and Bräunig, 2010), the depressor muscles begin to contract once the hindlegs have been levated into their cocked position, and continue to contract without moving the hindlegs. Second, if the muscles do act in this way, how are movements of the hindlegs restrained while the catapult is loaded? Third, what structures store the energy generated by these muscle contractions and what materials do they contain? Finally, how is the catapult triggered so that the two hindlegs extend together to produce a well-directed force?

ACKNOWLEDGEMENTS

I am indebted to Steve Shaw for his help throughout this work. I also thank colleagues in Dalhousie and Cambridge Universities for their many helpful suggestions and for their comments on the manuscript. Jo Riley also helped enormously with some of the data analyses.

FUNDING

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

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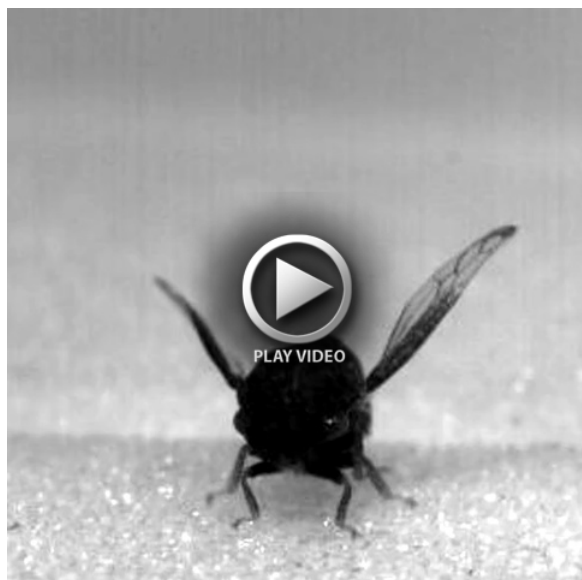
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Movie 1. A jump by *Carynota marmorata* captured at 5000 frames s^{-1} and replayed at 10 frames s^{-1} . The insect is viewed from underneath as it jumps from the front glass wall of the experimental chamber. The hindlegs slip as they are extended rapidly. See Fig. 4.



Movie 2. A side view of a jump by *Telamona compacta* captured at 5000 frames s^{-1} and replayed at 10 frames s^{-1} . See Fig. 6.



Movie 3. A head-on view of a jump by *Publilia concava* that is preceded by six cycles of wing flapping, but take-off is only achieved when the hindlegs propel a jump. Images were captured at 5000 frames s^{-1} and replayed at 10 frames s^{-1} . See Fig. 8.