

The effect of leg length on jumping performance of short- and long-legged leafhopper insects

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SUMMARY

To assess the effect of leg length on jumping ability in small insects, the jumping movements and performance of a sub-family of leafhopper insects (Hemiptera, Auchenorrhyncha, Cicadellidae, Ulopinae) with short hind legs were analysed and compared with other long-legged cicadellids (Hemiptera, Auchenorrhyncha, Cicadellidae). Two species with the same jumping characteristics but distinctively different body shapes were analysed: *Ulopa*, which had an average body length of 3 mm and was squat, and *Cephalelus*, which had an average body length of 13 mm with an elongated body and head. In both, the hind legs were only 1.4 times longer than the front legs compared with 1.9–2.3 times in other cicadellid leafhoppers. When the length of the hind legs was normalised relative to the cube root of their body mass, their hind legs had a value of 1–1.1 compared with 1.6–2.3 in other cicadellids. The hind legs of *Cephalelus* were only 20% of the body length. The propulsion for a jump was delivered by rapid and synchronous rotation of the hind legs about their coxo-trochanteral joints in a three-phase movement, as revealed by high-speed sequences of images captured at rates of 5000 s⁻¹. The hind tarsi were initially placed outside the lateral margins of the body and not apposed to each other beneath the body as in long-legged leafhoppers. The hind legs were accelerated in 1.5 ms (*Ulopa*) and 2 ms (*Cephalelus*) and thus more quickly than in the long-legged cicadellids. In their best jumps these movements propelled *Ulopa* to a take-off velocity of 2.3 m s⁻¹ and *Cephalelus* to 2 m s⁻¹, which matches that of the long-legged cicadellids. Both short-legged species had the same mean take-off angle of 56° but *Cephalelus* adopted a lower angle of the body relative to the ground (mean 15°) than *Ulopa* (mean 56°). Once airborne, *Cephalelus* pitched slowly and rolled quickly about its long axis and *Ulopa* rotated quickly about both axes. To achieve their best performances *Ulopa* expended 7 µJ of energy, generated a power output of 7 mW, and exerted a force of 6 mN; *Cephalelus* expended 23 µJ of energy, generated a power output of 12 mW and exerted a force of 11 mN. There was no correlation between leg length and take-off velocity in the long- and short-legged species, but longer legged leafhoppers had longer take-off times and generated lower ground reaction forces than short-legged leafhoppers, possibly allowing the longer legged leafhoppers to jump from less stiff substrates.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/211/8/1317/DC1>

Key words: kinematics, Auchenorrhyncha, Hemiptera, locomotion.

INTRODUCTION

Does leg length influence the jumping performance of small insects? In large animals that use direct muscle contractions to jump, the take-off velocity is limited by the amount of energy a muscle can generate; the higher the strain rate of a muscle, the less energy it can produce (Zajac, 1989). Longer legs provide higher lever arm ratios for the muscles powering a jump, allowing them to generate high centre of mass velocities while maintaining a low strain-rate and thus increasing the amount of energy in the jump (Alexander, 1995). In smaller animals, jumps are often powered by a catapult-like recoil of elastic structures (Bennet-Clark, 1990) and not by direct muscle contraction. Insects that use a catapult-like mechanism lock their joints before jumping and then contract their jumping muscles slowly to deform elastic structures within the legs or body. This strategy minimizes the strain rate of their muscles and thus maximizes the energy that the muscle can generate. Once the energy is stored, the insect then releases the locked joint, and the recoil of the elastic structure powers the jump (Bennet-Clark, 1990). In such a mechanism, take-off velocity should be independent of leg length because the energy released by these elastic structures is nearly independent of strain rate (Alexander, 1995; Bennet-Clark, 1990).

Although the net energy, and thus take-off velocity, should be unaffected by leg length, the increase in lever arm ratios caused by longer legs should reduce the centre of mass acceleration and increase the take-off time (Bennet-Clark, 1990). To test the prediction that leg length affects take-off time but not take-off velocity in catapult jumpers, we have analyzed the jumping kinematics of two species of short-legged insects and then compared their performance with longer legged species in the same family.

The widespread and diverse group of plant sucking bugs (Hemiptera, Auchenorrhyncha) contains some of the most accomplished jumpers amongst all insects. Froghoppers, which belong to one of the families (Cercopidae), accelerate their bodies in less than 1 ms to a take-off velocity of 4.7 m s⁻¹ and reach heights some 115 times their body length by exerting a force some 400 times their body mass (Burrows, 2003; Burrows, 2006). They achieve these remarkable feats of jumping even though they have only short hind legs, by storing energy in advance of the jump and then releasing it suddenly in a catapult-like action (Burrows, 2007c). Another family of these plant sucking bugs is the Cicadellidae or leafhoppers that contains some 22 000 known species distributed world wide (Dietrich, 2004). Most leafhoppers have hind legs that

are between two and three times longer than the other legs compared with 1.4 times in froghoppers (Burrows, 2007a; Burrows, 2007b). So long are the hind legs of some species that modifications to the head capsule are necessary to accommodate the hind legs when they are levated in preparation for a jump (Burrows, 2007a). The length of the hind legs also gives them a characteristic waddling gait when walking (Burrows, 2007b). One group of leafhoppers (sub-family Ulopinae), however, have short hind legs. By analysing the kinematics of these short-legged cicadellids, we show that they must use a catapult mechanism and that their take-off velocity in jumping matches that of the long-legged cicadellids, but that their take-off time is shorter. We then show that, across many leafhopper species, leg length is not correlated with take-off velocity, but is strongly correlated with the time required for take-off. This strongly supports the models for elastic recoil jumping (Alexander, 1995; Bennet-Clark, 1990). The longer acceleration time that nevertheless results in a similar take-off velocity means that long-legged leafhoppers generate lower ground reaction forces during a jump, and may therefore lose less energy than short-legged leafhoppers when jumping from a compliant leaf.

MATERIALS AND METHODS

Ulopa reticulata (Fabricius 1794) were collected near Godshill, Fordingbridge, Hampshire. In the laboratory they were maintained on *Erica*, the plant under which they were found. *Cephalelus angustatus* Evans were collected in the fynbos near Silvermines on the cape peninsula, Cape Town, South Africa. In the laboratory they were maintained at room temperature and fed on their natural host plants, cape reeds *Restio* (Restionaceae). Both species of leafhopper belong to the order Hemiptera, suborder Auchenorrhyncha, super-family Cicadelloidea, family Cicadellidae, sub-family Ulopinae.

Sequential images of jumps were captured at rates of 5000 s^{-1} with a Photron Fastcam 1024PCI high-speed camera [Photron (Europe) Ltd, Marlow, Bucks, UK] and with an exposure time of 0.03 or 0.05 ms. The images were fed directly to a laptop computer. Jumps were recorded by a camera placed in front of a chamber with a floor of high-density foam that measured $80\text{ mm}\times 80\text{ mm}\times 25\text{ mm}$ (width \times height \times depth). Within this chamber the insects were manoeuvred into position by delicate mechanical stimulation with a fine paintbrush and could jump in any direction. Selected sequences of images were analysed with Motionscope camera software (Redlake Imaging), or with Canvas X (ACD Systems of America, Miami, FL, USA). Movies of a jump by each species are included as Movies 1 and 2 in supplementary material.

The time at which the hind legs lost contact with the ground and the insect became airborne was designated as $t=0\text{ ms}$ so that different jumps could be compared and aligned. The acceleration period for a jump was defined from the first movement of the hind legs until they left the ground at take-off. Linear velocity was calculated as a rolling three-point average from successive frames around take-off. Energy lost to rotation was calculated by approximating the insect as a rod rotating about its transverse axis.

Photographs and anatomical drawings were made from both live and preserved specimens. Measurements are given as means \pm standard error of the mean (s.e.m.) and statistical trends were analyzed using a standard linear regression. Data are based on 16 jumps by five *Cephalelus* recorded at 32°C and ten jumps by five *Ulopa* recorded at 25°C . These temperatures reflected differences in the natural habitat of these species.

To compare the morphology of different species, measurements of the length of the hind legs were normalized by the cube root of

mass [length (in mm) $^3/\sqrt{\text{mass (in mg)}}$]. This prevents differences in body shape from artificially skewing data while still allowing a comparison of leg lengths in insects of different sizes.

RESULTS

Body shape

The *Ulopa* adults used here had a body mass of $2.1\pm 0.1\text{ mg}$ (mean \pm s.e.m.) and a body length of $3.1\pm 0.1\text{ mm}$ ($N=6$). The head was flattened at the front with eyes protruding both anteriorly and laterally (Fig. 1A). The pronotum was conspicuous and the hardened front wings covered the dorsal part of the thorax and abdomen, tapering posteriorly to give a pointed appearance to the posterior part of the body when viewed dorsally. The abdomen was clearly visible from a side view protruding ventrally. Hind wings were absent.

Cephalelus adults had a mass of $9.2\pm 0.6\text{ mg}$ (mean \pm s.e.m.) and a body length of $13.4\pm 0.4\text{ mm}$ ($N=9$). The body shape was distinctively long and thin, tapering gradually at both ends (Fig. 1B). The eyes were set at the posterior end of the elongated head that was some 5 mm long or 38% of the body length. The hardened front wings constituted 54% of the body length, covered the thorax behind the pronotum (the remaining 8% of body length) and the abdomen, so that only the wing tips protruded posteriorly. Hind wings were absent. This tapered body shape together with its brown colouration provided excellent camouflage on its host *Restio* plants by matching the cylindrical shape and size of the stems (culms). It could lie tightly apposed along the long axis of a stem so that it

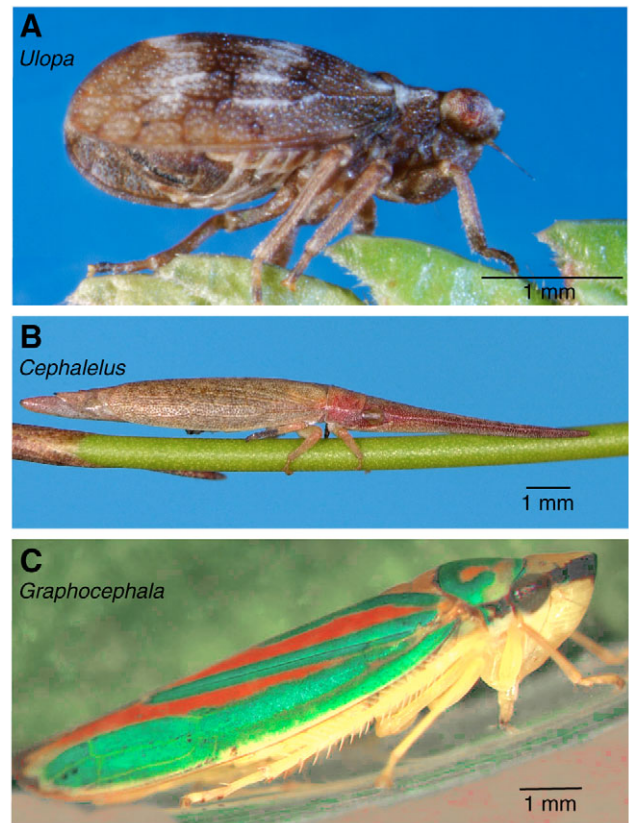


Fig. 1. Body form of short and long-legged leaf hoppers. (A) Side view of the short-legged *Ulopa* standing on its host plant *Erica*. (B) Side view of short-legged *Cephalelus* on its host plant *Restio*. (C) Side view of long-legged *Graphocephala fennahi*.

Table 1. Body form in short- and long-legged leafhoppers

Species (N)	Body mass (mg)	Body length (mm)	Hind leg (mm)		Ratio of leg lengths			Hind leg length (% of body length)	Normalized hind leg length (mm)/mass (mg) ^{0.33}
			Tibia	Femur	Front	Middle	Hind		
Short-legged									
<i>Cephalelus</i> (14)	9.2±0.56	13.4±0.4	1.3±0.02	0.8±0.02	1	1.1	1.4	20	1
<i>Ulopa</i> (7)	2.1±0.12	3.1±0.1	0.9±0.05	0.5±0.03	1	1.1	1.4	58	1.1
Long-legged*									
<i>Empoasca</i> (7)	0.86±0.72	3.5±0.03	1.5±0.05	0.7±0.05	1	1	2.1	82	2.3
<i>Aphrodes</i> (8)	18.4±1.3	8.5±0.22	3.8±0.06	2.2±0.03	1	1.2	2.2	84	2.3
<i>Cicadella</i> male (5)	10.9±0.5	6.4±0.16	3.1±0.06	1.6±0.1	1	1.1	1.9	93	2.1
<i>Cicadella</i> female (6)	19.0±1.1	9.2±0.33	3.8±0.05	2.0±0.1	1	1.1	1.9	82	2.2
<i>Graphocephala</i> (4)	13	13	4	2	1	1.2	2.9	91	2.6
<i>lassus</i> adults (7)	18.2±0.06	7.1±0.29	3.0±0.01	1.8±0.04	1	1.2	2.3	87	1.8
<i>lassus</i> nymphs (8)	9.0±0.08	5.7±0.28	2.0±0.15	1.3±0.05	1	1.2	2	73	1.6

*(from Burrows, 2007b).

looked like one of the small, brown sheaths that are the sole remnants of leaves in these plants.

Structure of the hind legs

The front legs of *Ulopa* were on average 1.3 mm long, the middle legs 1.4 mm and the hind legs 1.8 mm, so that the ratio of leg lengths was 1 front:1.1 middle:1.4 hind (Table 1). The femora of the hind legs were 14% longer than the middle and 23% longer than the front femora, and the hind tibiae were 31% longer than the middle and 35% longer than the front tibiae. Relative to the short body, the hind legs represented 58% of the body length. Relative to the cube root of the body mass, the hind leg length was 1.1.

The front legs of *Cephalelus* were on average 1.9 mm long, the middle legs 2.1 mm and the hind legs 2.6 mm, so that the ratio of leg lengths of 1 front:1.1 middle:1.4 hind was the same as in *Ulopa* (Table 1). The longer hind legs resulted from femora that were 11% longer than the middle and 23% longer than the front femora, and tibiae that were 25% longer than the middle and 33% longer than the front tibiae. The hind legs were, however, very short relative to the long body and represented only 20% of the body length. Relative to the cube root of body mass, the hind leg length was 1.0, and thus very close to the value for *Ulopa* (1.1). Both values are therefore distinct from leafhoppers with long hind legs such as *Graphocephala* (Fig. 1C) (Burrows, 2007b) in which

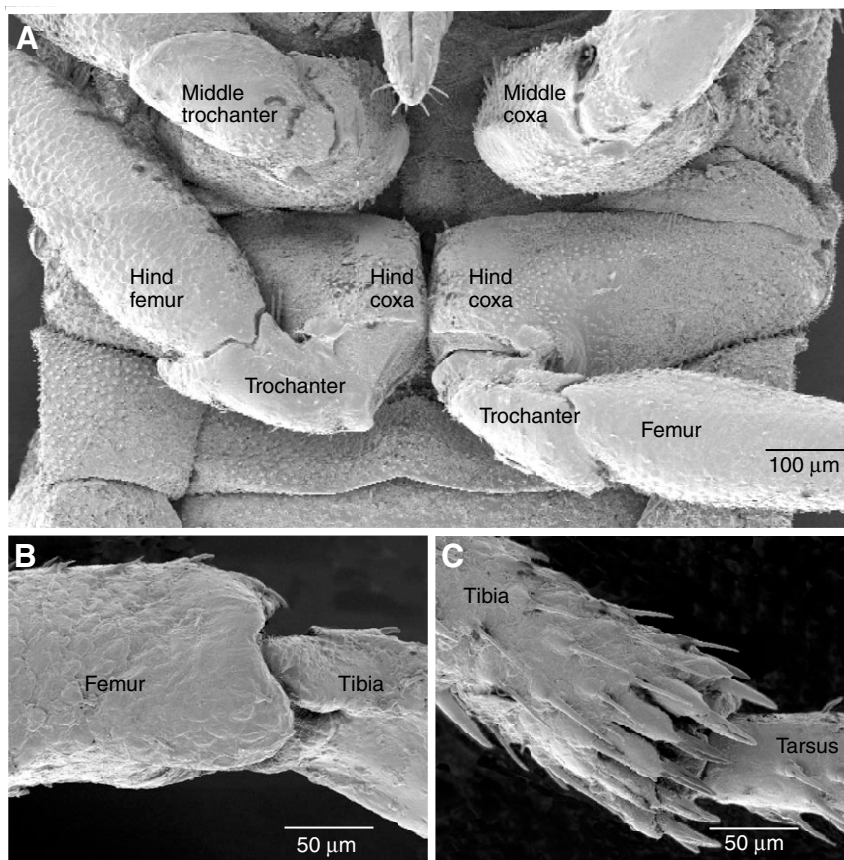


Fig. 2. Scanning electron micrographs of *Ulopa* to show the key structures of the hind legs for jumping. (A) The proximal joints of the middle and hind legs viewed ventrally. The hind coxae extend the width of the metathorax and are apposed at the ventral midline; the middle coxae are more widely separated. The right hind leg is in the levated position ready for jumping; the left hind leg is depressed. Anterior is to the top. (B) The femoro-tibial joint of a hind leg viewed from its lateral side showing the lack of specialisations for jumping and the absence of femoral spines. (C) The tibio-tarsal joint of a hind leg viewed ventrally to show the semi-circular array of spines.

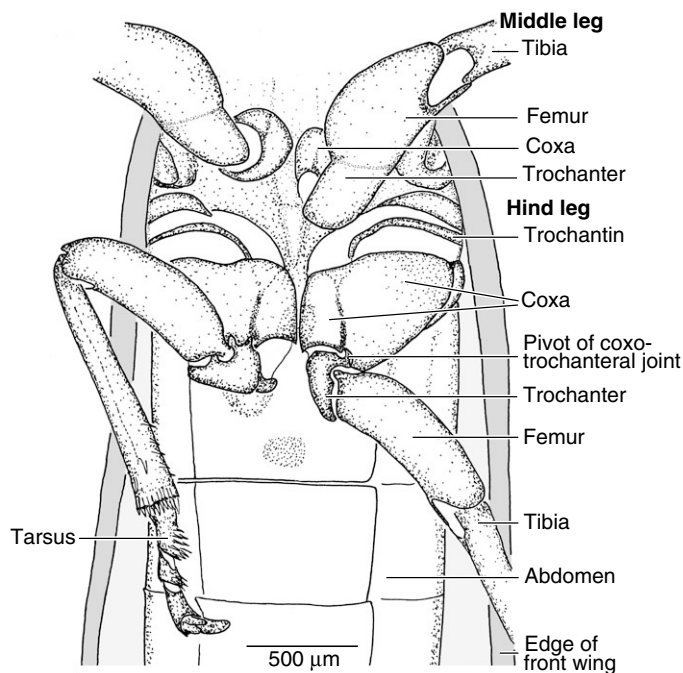


Fig. 3. Drawing of a ventral view of *Cephalelus* to show the structures involved in jumping. The right hind leg is levated at the coxo-trochanteral joint and the tibia partially flexed about the femur. The left hind leg is fully depressed and extended, and its distal parts are omitted. The middle legs are rotated forwards to reveal the trochantin of each hind leg. Anterior is to the top.

these values range from 1.6 to 2.3 in five different species (Table 1).

In both species, the coxae of the hind legs were larger than those of a front or middle leg. They were closely apposed to each other at the midline and extended from the midline to the lateral edge of the metathorax (Fig. 2A, Fig. 3). They could rotate forwards and backwards only through a small angle about the metathorax, and they lacked the linking structure of other adult leafhoppers in which a protrusion from one medial surface inserts into a socket on the other coxa (Burrows, 2007a). The ventral surface of a hind coxa had two prominent arrays of stout hairs that would appear to act as proprioceptors in jumping. The first consisted of a group of four hairs in a ventral depression into which the femur located when the coxo-trochanteral joint was fully levated. These hairs will be distorted by the femur in this position and could therefore signal full levation of a hind leg. The second consisted of a group of six longer and thinner hairs at the anterior edge of the coxa that are likely to be distorted by contact with the trochantin when the coxa is moved forwards.

The trochanter pivoted with the coxa about a ventral (Fig. 2A, Fig. 3) and a dorsal articulation in which curved horns of the trochanter inserted into sockets on the coxa. A group of hairs on the ventral trochanteral horn should be distorted by contact with the coxa when the trochanter is fully levated. The trochanter can be levated and depressed through an angle of approx. 130° about the coxa.

The hind tibia was 60–80% longer than the hind femur in both species (Table 1). The femoro-tibial joint showed no outward specialisations and lacked femoral spines (Fig. 2B). The tibia could extend and flex through an angle of approx. 160 – 170° about the femur, in the same plane as the levation and depression movements of the trochanter. The tibiae have no longitudinal rows of prominent

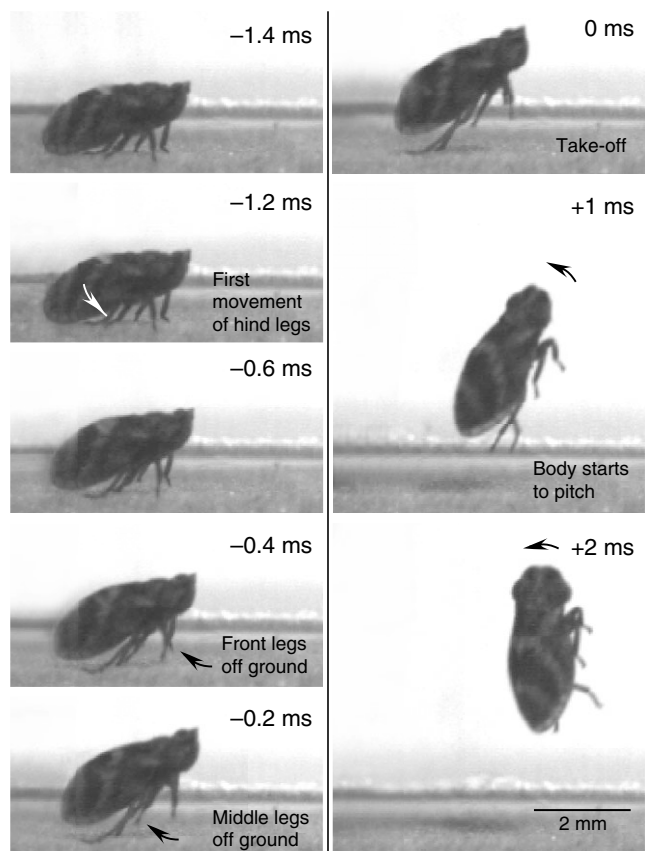


Fig. 4. Images of a jump by *Ulopa* viewed from the side. The images at the times indicated are arranged in two columns with the bottom left hand corner providing a constant reference point in this and in Figs 5, 6. The first movements of the hind legs (arrow) began 1.2 ms before take-off. The front and middle legs (arrows) lost contact with the ground before take-off. After take-off the body began to rotate backwards about its longitudinal axis. Images were captured at 5000 s^{-1} and with an exposure time of 0.05 ms.

spines that characterise most other leafhoppers. Short spines were, however, present at the ventral surface of the tibio-tarsal and proximal tarsal joints, which could increase traction with the ground when jumping (Fig. 2C, Fig. 3).

Jumping movements

The movements of the legs and the body of *Ulopa* and *Cephalelus* during jumping were determined from high-speed images captured as the insects jumped from the horizontal and viewed from the side (Figs 4, 5), from in front (Fig. 6A) and underneath (Fig. 6B). As in leafhoppers with long hind legs (Burrows, 2007a; Burrows, 2007b), three phases of a jump were seen that are represented by drawings in Fig. 6C.

First, in preparation for a jump, the hind legs were drawn forward into their fully levated position by rotation about their coxo-trochanteral joints and the tibiae were flexed about the femora. The tarsi of the two hind legs were placed on the ground outside the lateral edges of the body so that they were well separated and therefore unable to touch each other (Fig. 6). This contrasts with the placement of the hind legs of long-legged leafhoppers where the tarsi were positioned directly beneath the body so that they, and distal ends of the tibiae, touched (Burrows, 2007a; Burrows, 2007b). The front and middle legs of *Ulopa* and *Cephalelus* did

not consistently change their posture from that adopted during any preceding behaviour. The front legs pointed forwards whereas the middle and hind legs pointed backwards. The movements of the front and middle legs could set the angle of the body relative to the ground, but in *Cephalelus* their scope for effecting such changes was limited by the elongated shape of the body; if the front of the body were raised too far the abdomen would be pressed against the ground. The head of *Cephalelus* could, however, most obviously be moved relative to the rest of the body by an articulation at the pronotum so that at the end of this preparatory phase of the jump the angle of the head-pronotum joint was 173° (Fig. 5).

Second, the hind legs were held motionless in this fully levated position for periods up to 200 ms but the front and middle legs moved to adjust the position of the body.

Third, the jump movement itself, which resulted from a rapid depression of the coxo-trochanteral joints and an accompanying extension of the femoro-tibial joints. The coxo-trochanteral joint of *Cephalelus* was rotated at $70\,000\text{ deg. s}^{-1}$ and the femoro-tibial joint at $54\,000\text{ deg. s}^{-1}$ during this phase of the movement. These movements of the hind legs gradually raised the body from the ground and as a consequence the front and middle legs lost contact with the ground before the hind legs. In *Ulopa*, the first movements of the hind legs from their starting position occurred $1.5\pm 0.04\text{ ms}$ ($N=6$) and in *Cephalelus* $2.1\pm 0.08\text{ ms}$ ($N=14$) before take-off and were the result of a depression movement of the coxo-trochanteral joints from their fully levated positions. This period represents the take-off time during which the body was accelerated by the movements of the hind legs. The movements of the two hind legs appeared to occur at the same time within the 0.2 ms resolution provided by the $5000\text{ images s}^{-1}$ frame rate of the camera. The tarsi of the two hind legs remained placed outside the lateral limits of the body. Once airborne they moved medially so that they touched and then crossed. The angle between the head and the

thorax of *Cephalelus* gradually increased in preparation for a jump so that at take-off it was 180° and the whole of the body was thus aligned.

The take-off angle in both species ranged from 45° to 70° with a mean of $56.3\pm 2.5\text{ ms}$ ($N=14$), but the attitude of the body relative to the ground was different in each. *Ulopa* assumed a high angle of the body to the ground [mean of $56.1\pm 2.3^\circ$ ($N=10$)] whereas *Cephalelus* adopted a low angle [mean of $14.5\pm 2.1^\circ$ ($N=10$)] (Fig. 7A, Fig. 8A). Once airborne there were also differences between the two species in the rate and direction of rotation of the body (Figs 4, 5, Fig. 7B, Fig. 8B). *Ulopa* often rotated quickly about roll (longitudinal) and pitch (transverse) axes simultaneously; by contrast, *Cephalelus* sometimes rolled quickly about its roll axis but only slowly about its pitch axis.

This pattern of leg movements propelled *Ulopa* to a take-off velocity of $1.9\pm 0.2\text{ m s}^{-1}$ (mean of the peak velocity in five jumps) reaching a velocity of 2.3 m s^{-1} in its best jumps (Fig. 7B, Table 2). *Cephalelus* achieved a take-off velocity of $1.6\pm 0.2\text{ m s}^{-1}$ ($N=6$) with a best performance of 2 m s^{-1} (Fig. 8B, Table 2). The peak velocity was attained just before take-off but was usually maintained for several milliseconds afterwards, before declining gradually.

Assuming that a jump did not experience any slowing due to wind resistance, the distance and height achieved are given by Eqn 1 and 2 (Alexander, 1968):

$$s = U \cos \theta (2U \sin \theta / g), \quad (1)$$

$$h = (U \sin \theta)^2 / 2g, \quad (2)$$

where s is distance jumped, h is maximum height reached, U is instantaneous velocity at take-off, θ is take-off angle and g is acceleration due to gravity (9.81 m s^{-2}).

Taking the mean take-off velocity (1.9 m s^{-1}) and the mean angle at take-off (56.3°), *Ulopa* should jump a distance of 340 mm and

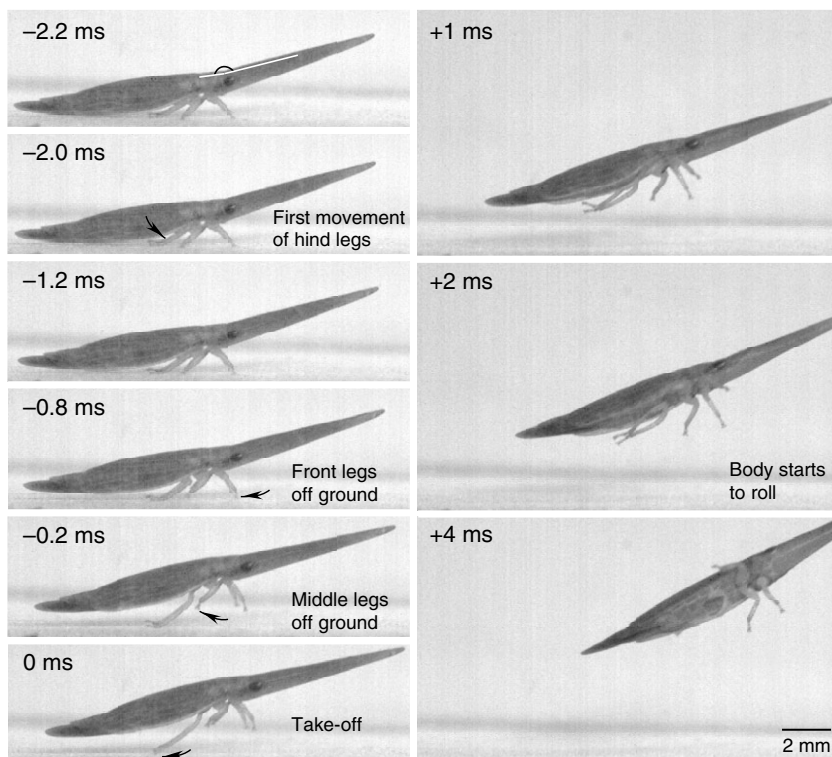


Fig. 5. Images of a jump by *Cephalelus* viewed from the side and captured at 5000 s^{-1} and each with an exposure time of 0.03 ms. The first movement of a hind leg occurred 2 ms before take-off (arrow). The front and middle legs (arrows) lost contact with the ground before take-off. After take-off the body began to rotate around its longitudinal axis. The lines on the first frame (-2.2 ms) indicate how the angle between the head and the pronotum was measured.

would reach a height of 127 mm. At its fastest take-off velocity the distance would be 496 mm and the height 187 mm. *Cephalelus* with its lower take-off velocities should do worse. With the mean take-off velocity (1.6 m s^{-1}) and a mean angle at take-off (56.3°) *Cephalelus* should jump a distance of 240 mm and would reach a height of 90 mm. At its fastest take-off velocity the distance would increase to 376 mm and the height to 141 mm.

The wind resistance experienced by these differently sized insects, which is not considered in these equations, is likely to curtail the real heights and distances achieved to different extents. Flea beetles (*Psylloides affinis*), which are smaller than both *Cephalelus* and *Ulopa*, lose 40% of their jumping range to drag (Brackenbury and Wang, 1995); whereas froghoppers, which are heavier than both *Cephalelus* and *Ulopa* lose only 25% of their jumping range to drag [estimates by Vogel, (Vogel, 2005) based on data in Burrows (Burrows, 2003)]. As *Cephalelus* and *Ulopa* are intermediate in size between these two examples, they may be assumed to lose between 25% and 40% of their energy to drag, with the larger *Cephalelus* losing less energy than the smaller *Ulopa* (Bennet-Clark and Alder, 1979; Vogel, 2005).

Jumping performance

Jumping performance was calculated from the data obtained from the high-speed images (Table 2). The time from the first visible

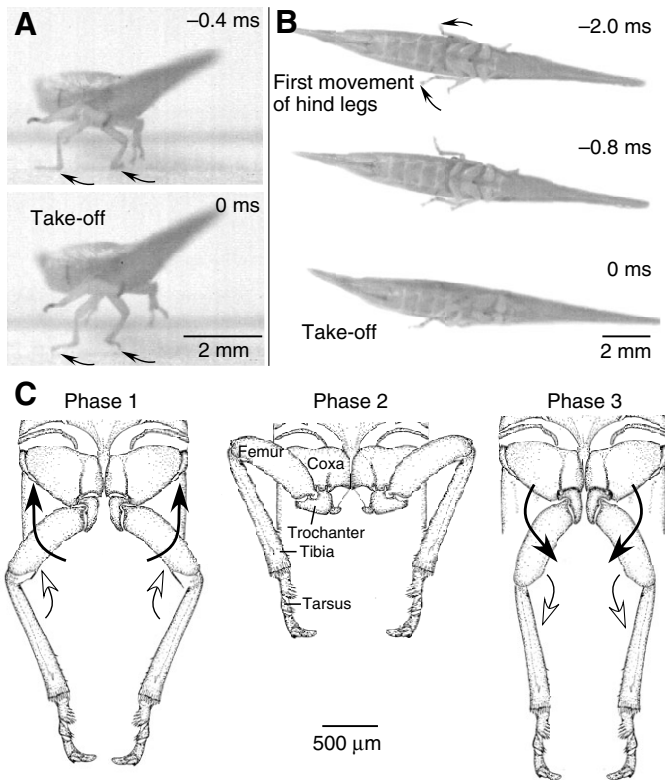


Fig. 6. Jumping in *Cephalelus*. (A,B) Placement of the hind tarsi and leg movements in a jump. (A) Two frames from a jump toward and to the right of the camera. The hind tarsi were placed on the ground lateral to the left and right edges of the body (arrows) and remained in that position at take-off. (B) A jump from the vertical, glass front of the chamber viewed from underneath. The tarsi of the hind legs (arrows) are again placed outside the lateral outline of the body and thus do not touch. The first movements of the hind legs began 2 ms before take-off. Images were captured at 5000 s^{-1} and with an exposure time of 0.03 ms. (C) Drawings of the hind legs of *Cephalelus* to show their movements during the three phases of a jump.

movement of the hind legs until the insect became airborne defined the period over which the body was accelerated. In *Ulopa*, the average acceleration over this whole period was 1267 m s^{-2} (average of six jumps) rising to 2300 m s^{-2} in the best jumps. In *Cephalelus*, the lower take-off velocity and its longer acceleration period meant that its acceleration was lower at 762 m s^{-2} (average of six jumps), rising to 1000 m s^{-2} in its best jumps. The energy required to achieve these performances depended on body mass so that the best jumps of *Ulopa* required $7 \mu\text{J}$, but in the much heavier *Cephalelus* $23 \mu\text{J}$ were required. The power output in a jump depends on the time during which the energy is expended. In the 1.5 ms that *Ulopa* took to accelerate its body, the power output was 2.7 mW, over doubling to 7.0 mW in its best jumps. In *Cephalelus* the comparable values were 5.7 and 12 mW. Similarly, the force exerted during the best jumps by *Ulopa* was 5.8 mN, and was 11 mN in the heavier *Cephalelus*.

Both *Cephalelus* and *Ulopa* require large amounts of power for jumping relative to the mass of their jumping muscles; we calculate

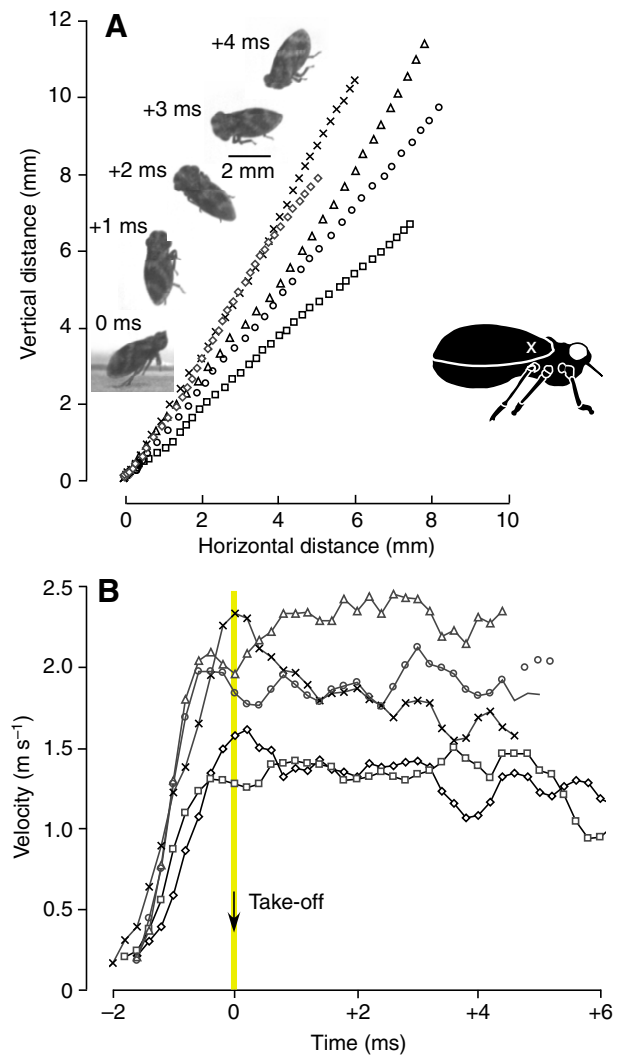


Fig. 7. Trajectories and velocities of five jumps by *Ulopa*. (A) Trajectories of five jumps. The images of *Ulopa* at the times indicated are from the jump plotted as the diamond symbols and show that it rotated around both its longitudinal and transverse axes. (B) Velocity of the same five jumps, each plotted as a three-point rolling average against time, of a point on the body roughly corresponding to its centre of gravity and indicated by the cross on the cartoon in A.

these requirements as 5600 and 12000 W kg⁻¹ respectively (Table 2). Both power requirements are an order of magnitude higher than muscle could produce by direct contraction even under optimal conditions with assistance from series elastic elements, indicating that the jumps of these short-legged leafhoppers are powered by elastic recoil of a catapult-like mechanism (Bennet-Clark, 1990; Josephson, 1993; Roberts, 2002).

Changing the temperature had no influence on the take-off velocity achieved by leafhoppers using a catapult mechanism. At 10°C the long-legged leafhopper *Aphrodes* (of the *makarovi* Zachvatkin, 1948/*bicinctus* (Schrank) group) achieved an average take-off velocity of 1.8±0.1 m s⁻¹ (N=11) and at 25°C an average take-off velocity of 1.9±0.1 m s⁻¹ (N=11). The different temperatures at which *Cephalelus* and *Ulopa* jumped (25 or 32°C) would not therefore be expected to have any effect on their take-off velocity.

Body rotation

Once airborne there were differences between the two species in the rate and direction of rotation of the body (Figs 4, 5, Fig. 8B, Fig. 9B). *Ulopa* rotated at rates of up to 33 000 deg. s⁻¹ (or 92 Hz), giving it the fastest rotation rate of any Homopteran hitherto analyzed (Brackenbury, 1996; Burrows, 2007b). This angular velocity

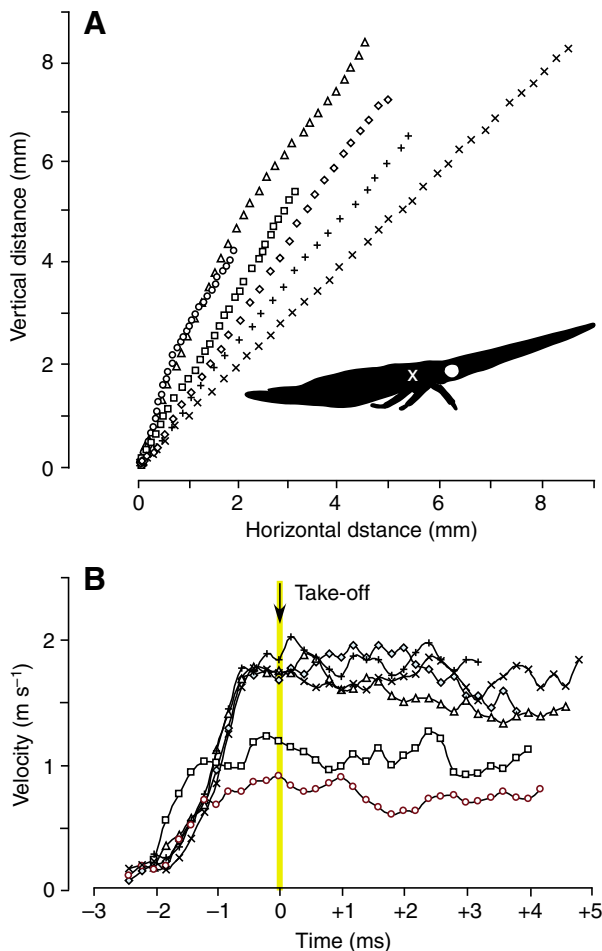


Fig. 8. Trajectories and velocities of five jumps by *Cephalelus*. (A) Trajectories of five jumps. (B) Velocities of the same five jumps, plotted as a three-point rolling average against time, of a point on the body indicated by the cross on the cartoon. Peak velocity, measured as in Fig. 7, was reached less than 1 ms before take-off.

Table 2. Jumping performance of short- and long-legged leafhoppers

Species (N)	Formulae	t	Time to take-off (ms)	Take-off linear velocity (m s ⁻¹)	Take-off angular velocity (deg. s ⁻¹)	Mass (mg)	Length (mm)	Acceleration (m s ⁻²)	Acceleration (g)	Translational energy (μJ)	Rotational energy (μJ)	Power (mW)	Force (mN)	Energy/mass (μJ mg ⁻¹)	Power/muscle mass* [mW mg ⁻¹ (W kg ⁻¹)]
				V	57.3ω	m	l	a=V/t	g=a/9.86	e=0.5 mV ²	e ^{rot} =m ² ω ² /24	p=(e+e ^{rot})/t	F=ma	(e+e ^{rot})/m	p/(0.11m)
Short-legged															
<i>Cephalelus</i>															
Average (6)		2.1±0.08	2	1.6±0.2	2624	9.2	13.4	762	77	12	0.14	5.7	7.0	1.3	5.6 (5600)
Best			2	2	4003	11.4		1000	101	23	0.42	12	11	2.0	9.3 (9300)
<i>Ulopa</i>															
Average (6)		1.5±0.04	1	1.9±0.2	28190	2.1	3.1	1267	128	3.8	0.20	2.7	2.7	1.9	12 (12000)
Best			1	2.3	33347	2.5		2300	233	6.6	0.34	7.0	5.8	2.8	25 (25000)
Long-legged															
<i>Empoasca</i> (7) [†]															
Average (43) [†]		4.7±0.1		1.1±0.11	2177 [†]	0.86	3.5	234	24	0.5	0.001	0.1	0.2	0.6	1.2 (1200)
<i>Cicadella</i> (♂) (10) [†]		4.4±0.18		2.5±0.09	3846	18.4	8.5	568	58	58	0.25	13	11	3.1	6.5 (6500)
<i>Graphocephala</i> (16)		6.4±0.21		1.2±0.13	3505	10.9	6.4	188	19	7.8	0.07	1.2	2.0	0.7	1.0 (1000)
<i>lassus</i> (nymph) (1)		5.6±0.25		1.6±0.07	-	13	9.0	286	29	17	-	3.0	3.7	1.3	2.1 (2100)
		2.5		2	-	4	4.3	800	81	8	-	3.2	3.2	2.0	7.3 (7300)

*Extensor muscle mass is approximately 11% of body mass.

[†]Data from Burrows (Burrows, 2007b).

[‡]Data from Brackenbury (Brackenbury, 1996).

required 0.20 μJ of energy, increasing the energy requirements for a jump by 5%. The elongated body of *Cephalelus* pitched at a much slower rate of 4000 deg. s^{-1} (11 Hz) and required only an additional 0.14 μJ of energy, which increased the energy requirements for a jump by about 1%. In some jumps, *Cephalelus* also rolled about its longitudinal axis at angular velocities as high as the rotation rate of *Ulopa*, but in others rolled very little. *Cephalelus* had a low moment of inertia about its longitudinal axis so that the energy requirements were low. Neither species used its front wings to provide stabilisation and prevent rotation once airborne.

DISCUSSION

The leafhoppers, *Ulopa* and *Cephalelus*, studied here have shorter hind legs than other cicadellid leafhoppers and yet achieve comparable take-off velocities (1.6 m s^{-1} and 1.9 m s^{-1} , respectively) compared with 1.6 m s^{-1} and 1.2 m s^{-1} for the long-legged *Graphocephala* and *Cicadella* (Burrows, 2007b). Normalised relative to the cube root of their body mass, the hind legs of *Cephalelus* and *Ulopa* have values of 1 and 1.1 compared with 1.6–2.3 in long-legged cicadellids. Their short hind legs allow them to accelerate their bodies in only 1.5 ms (*Ulopa*) or 2 ms (*Cephalelus*) and thus more quickly than the 3–5 ms acceleration period of long-legged leafhoppers (Table 2). The length of the hind legs in leafhoppers is therefore not correlated with take-off velocity, and longer legs do not lead to greater take-off velocities (Fig. 9A). Nevertheless, longer legs are correlated with longer take-off times (Fig. 9B). These two relationships, and the large power requirements, are consistent with these insects storing elastic energy in preparation for a jump and then releasing it suddenly, because leg length has

little effect on the amount of energy that is released but does affect the amount of time required to reach take-off (Bennet-Clark, 1990).

Neither *Ulopa* nor *Cephalelus* opened their front wings when airborne to stabilise their movements, in contrast to the long-legged cicadellids which often opened and flapped their wings. Furthermore, the short hind legs apparently could offer little effect as rudders as they trailed underneath the body in the air. As a consequence *Ulopa*, in particular, spun at high frequencies about the transverse and longitudinal axis of its body, losing as much as 5% of its kinetic energy to rotation. The long and thin body of *Cephalelus* meant that it spun more slowly about its transverse axis, losing little energy to rotational kinetic energy of the body.

Since having short hind legs reduces the time required to take-off, does not appear to change the leg depression and extension kinematics and incurs no penalty to take-off velocity, what advantage is gained by having long hind legs?

Why have short rather than long legs?

The long-legged leafhoppers in general have lower ground reaction forces than those with shorter hind legs [table 2 (Alexander, 1995)] and this may allow them to jump more effectively from less stiff substrates. When one of these plant sucking insects jumps from its host plant, energy is lost to bending the leaf or stem beneath it. Different parts of a plant have different stiffness, with the stem in general being stiffer than the leaves (Niklas, 1999). The less stiff the substrate, the more energy is lost. Longer legs should reduce the energy lost to bending the leaf, and thus allow an insect to reach high take-off velocities on leaves that are less stiff. An insect that jumps from plant stems, however, can have shorter legs because the stem is much more resistant to bending. *Cephalelus* jumps from the stiff cylindrical stems of *Restio* plants whereas the long-legged leafhoppers are generally found on the leaves of a variety of plants.

Energy losses due to leaf elasticity could be quite significant to jumping insects. Assuming a leaf petiole is a linear spring, the energy lost to leaf bending can be approximated as $1/2 \times \text{ground reaction force}^2 / \text{leaf stiffness}$. Petiole stiffness can be estimated by assuming the leaf is a cantilever beam with a stiffness $3 \times \text{flexural rigidity} / \text{length}^3$ (Niklas, 1999). For a 10 cm leaf petiole, the flexural rigidity is approximately 10^{-3} N m^2 (Niklas, 1999), resulting in a stiffness of approximately 3 N m^{-1} . A short-legged *Cephalelus* jumping from the end of a 10 cm petiole with a ground reaction force of 7 mN would then lose 8 (66%) of its 12 μJ of available energy to bending of the leaf. A male, long-legged *Cicadella*, however, jumping from the same petiole generates a ground reaction force of only 2 mN and thus loses only 0.7 (9%) of its available 8 μJ of energy to leaf bending. Consequently, the long legs of *Cicadella* enable it to achieve a higher take-off velocity when jumping from the end of a 10 cm petiole than could the short-legged *Cephalelus* of similar mass. The advantage would be even greater when jumping from a leaf lamina which is less stiff.

Longer legs do, however, require more structural reinforcement than shorter legs. Although the maximum bending moment on the leg is independent of its length and the compressive forces are inversely proportional to length (Bennet-Clark, 1990), the tendency of the leg to buckle is proportional to the square of length (Popov, 1990). Thus, despite lower compressive stresses, and similar bending stresses, longer legs will have to be more reinforced against buckling.

Long legs may also be used as energy stores. In reaction to a given bending moment, longer legs deform more than shorter ones (Popov, 1990), possibly providing an additional energy store, similar to the way *Prosarthria* use bending of the tibiae to store and release energy (Burrows and Wolf, 2002). If the longer legged

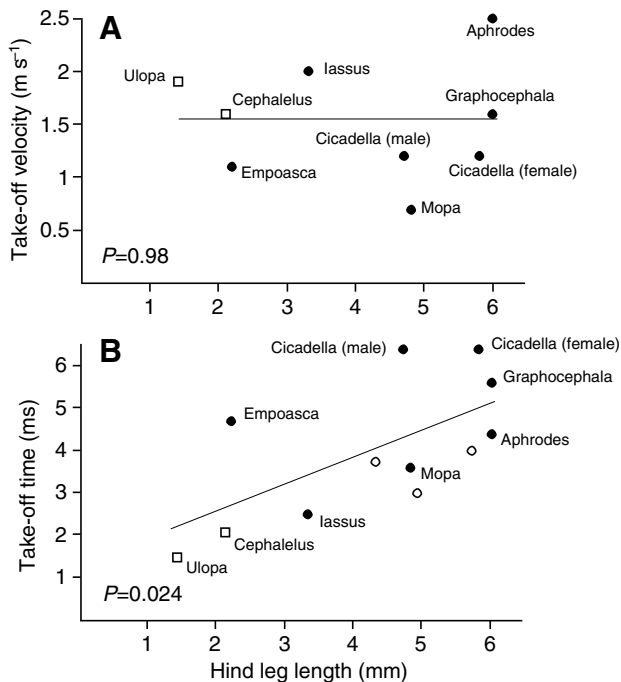


Fig. 9. Length of the hind legs and jumping performance in short- and long-legged leaf hoppers. (A) Length of hind legs is not correlated with take-off velocity [peak take-off velocity averaged across a number of jumps (see Table 2) for each species]. The two short-legged leaf hoppers are plotted as open squares; the six long-legged species as filled circles. (B) Leg length is linearly correlated with take-off time. The same species as in A are shown, together with three unidentified long-legged species (open circles). Both data fits were generated with a standard linear regression.

leafhoppers are using their hind legs as energy stores, then the prediction follows that their non-leg energy stores, which have yet to be identified, should be proportionally smaller than those of the short-legged leafhoppers. This is because the take-off velocities of both groups of insects are similar.

Long legs allow some insects to power their jumps by direct muscle contraction. This is the method used by bush crickets (Burrows and Morris, 2003), which proportionately have much longer hind legs than their close relatives the grasshoppers. Bush crickets can power jumps by extension movements of the tibia without first flexing the tibia fully about the femur, but locusts have to flex their tibiae fully to generate a powerful jump. Using long legs in this way gets round the problem of the substantial time it can take to load a catapult mechanism. In froghoppers, for example, the muscles providing the power can contract for several seconds before a jump is released (Burrows, 2007c). Short preparation times thus become possible with long hind legs and may have evolved to allow an emergency jump that is driven by direct muscle contraction. These jumps would have lower take-off velocities but may still be sufficient to generate a controlled fall from a plant and thus an effective escape. In the long-legged leafhoppers the hind legs are always moved into their fully levated position before jumping, and recordings from muscles indicate at least short periods of activity occur before a jump is released (Burrows, 2007a). Thus, it would seem that even with long legs, leafhoppers have to store energy before a jump can be generated.

Differences in leg length may also assist behaviour other than jumping. The hind legs are used in grooming, walking, kicking and, in some species, swimming. The different requirements for these movements may explain differences in the leg lengths. Specifically in leafhoppers, longer legs would allow more of the body to be anointed with brochosomes (Rakitov, 2000) during grooming, or to reach further during kicking. Regardless of the evolutionary demands, there does not appear to be a design conflict between these other movements and take-off velocity in jumping.

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