

## Jumping mechanisms and performance of pygmy mole crickets (Orthoptera, Tridactylidae)

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### SUMMARY

Pygmy mole crickets live in burrows at the edge of water and jump powerfully to avoid predators such as the larvae and adults of tiger beetles that inhabit the same microhabitat. Adults are 5–6 mm long and weigh 8 mg. The hind legs are dominated by enormous femora containing the jumping muscles and are 131% longer than the body. The ratio of leg lengths is: 1:2.1:4.5 (front:middle:hind, respectively). The hind tarsi are reduced and their role is supplanted by two pairs of tibial spurs that can rotate through 180 deg. During horizontal walking the hind legs are normally held off the ground. Jumps are propelled by extension of the hind tibiae about the femora at angular velocities of 68,000 deg s<sup>-1</sup> in 2.2 ms, as revealed by images captured at rates of 5000 s<sup>-1</sup>. The two hind legs usually move together but can move asynchronously, and many jumps are propelled by just one hind leg. The take-off angle is steep and once airborne the body rotates backwards about its transverse axis (pitch) at rates of 100 Hz or higher. The take-off velocity, used to define the best jumps, can reach 5.4 m s<sup>-1</sup>, propelling the insect to heights of 700 mm and distances of 1420 mm with an acceleration of 306 g. The head and pronotum are jerked rapidly as the body is accelerated. Jumping on average uses 116 µJ of energy, requires a power output of 50 mW and exerts a force of 20 mN. In jumps powered by one hind leg the figures are about 40% less.

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Key words: kinematics, locomotion, walking.

### INTRODUCTION

Jumping as a means of escaping from predators, launching into flight or merely increasing the speed of locomotion has evolved many times in insects so that it is part of the behavioural repertoire of species in many different insect orders. A diverse range of mechanisms are used but the most widespread is to propel jumps by rapid movements of the legs (typically the hind legs). The most adept jumping insects that use legs as the propulsive mechanism are found among the hemipteran bugs, with the froghopper *Philaenus spumarius* and the planthopper *Issus coleoptratus* currently reigning as champions among all insects (Burrows, 2003; Burrows, 2006; Burrows, 2009). Both use catapult mechanisms but each has its own set of particular specialisations in the mechanics of its hind legs, the arrangements and actions of its muscles and in its motor patterns to generate such supreme performances. Other jumping insects from different orders include fleas (Siphonaptera) (Bennet-Clark and Lucey, 1967; Rothschild et al., 1972), flea beetles (Coleoptera) (Brackenbury and Wang, 1995), flies (Diptera) (Card and Dickinson, 2008; Hammond and O'Shea, 2007; Trimarchi and Schneiderman, 1995), ants (Hymenoptera) (Baroni et al., 1994; Tautz et al., 1994) and stick insects (Phasmida) (Burrows and Morris, 2002). Some of the most accomplished jumping insects are the locusts and grasshoppers, and the bush crickets within the order Orthoptera. They illustrate the two basic mechanisms of jumping propelled by legs that are found in all insects.

First, desert locusts, *Schistocerca gregaria* (suborder Caelifera, family Acrididae), use a catapult mechanism to jump a horizontal distance of approximately 1 m from a take-off velocity of 3.2 m s<sup>-1</sup>

(Bennet-Clark, 1975). Their large body weighing 1.5–2 g is accelerated in 20–30 ms (Brown, 1967), requiring 9–11 mJ of energy. The high velocity and the power output required for such movements could only be produced if the power-producing muscles in the hind femora contract slowly and the force they generate is stored in distortions of cuticle (Burrows, 1995; Heitler and Burrows, 1977). The sudden release of this stored energy by recoil of the cuticular energy stores is then able to extend the hind tibiae rapidly and accelerate the locust to a high take-off velocity. The false stick insect *Prosarthria teretirostris* (suborder Caelifera, family Proscopiidae) has a much more elongated body with thin hind legs that lack many of the structural specialisations of locust hind legs but still uses a catapult mechanism to propel its jumps. The males, which weigh 0.28 g, achieve take-off velocities of 2.5 m s<sup>-1</sup> that propel the body a forward distance of 0.9 m (Burrows and Wolf, 2002).

Second, bush crickets (suborder Ensifera, family Tettigoniidae) are also accomplished jumpers but they rely on leverage provided by their very long hind legs. Contractions of the muscles in their hind femora directly control the long levers provided by their exceptionally elongated hind legs so that energy storage mechanisms are not required (Burrows and Morris, 2003). The resulting jumps by a male bush cricket *Pholidoptera griseoptera* achieve a lesser jumping performance with a take-off velocity of 1.5 m s<sup>-1</sup> that propels the 0.4 g body forwards a distance of 0.3 m.

Most notable among the other groups within the Orthoptera with species that are reported to jump are the pygmy mole crickets (suborder Caelifera, family Tridactylidae). They are considered to

represent the most basal lineage of the true grasshoppers (Flook et al., 1999; Flook and Rowell, 1997), and despite their common name are not closely related to true crickets or mole crickets. These insects are only a few millimetres long but are widely distributed across the warmer parts of the globe. They build horizontal galleries beneath the surface of damp substrates associated with nearby water, which can be intermingled with the vertical tunnels of predatory larvae and adults of tiger beetles (Coleoptera, Cicindellidae). To understand how they jump to escape these and other hazards, this investigation has analysed the structure of the hind legs and the kinematics of the jumping movements. It is shown that pygmy mole crickets have unique and remarkable specialisations of their hind legs which have enormous femora and in which the role of the tarsi is subsumed by two pairs of apical and sub-apical tibial spurs. During horizontal walking the hind legs are held clear of the ground and do not therefore contribute. The jumps, propelled by the hind legs, achieve take-off velocities of  $5.4\text{ m s}^{-1}$ , which match the highest values recorded in any insect (Burrows, 2009), and distances of 1.4 m or 250 times their body length. Many jumps are propelled by just one hind leg. The take-off angles are steep so that once airborne the body rotates backwards about its transverse axis.

## MATERIALS AND METHODS

Pygmy mole crickets *Xya capensis* var. *capensis* (Saussure 1877) were collected from three localities in the Western Cape Province, South Africa; in moist clay banks surrounding a dam on the campus of the University of Cape Town (33.95°S, 18.46°E), on the banks of a lake at Worcester (33.63°S, 18.46°E), and from sandy margins of the Silver Mine Reservoir on the Cape Peninsula (34.07°S, 18.40°E). The dimensions of the burrows of *X. capensis* and the cicindellid beetle *Lophyra capensis* that shared the same microhabitat at the University of Cape Town locality were measured with digital callipers. The density of tiger beetle tunnels was measured in ten  $1\text{ m} \times 1\text{ m}$  quadrats.

Sequential images of jumps were captured at rates of  $5000\text{ s}^{-1}$  and with an exposure time of 0.03 ms with a single Photron Fastcam 1024 PCI camera [Photron (Europe) Ltd, Marlow, Bucks, UK] that fed images directly to a computer. One hundred and twenty one jumps by 33 adult pygmy mole crickets were captured at temperatures of 28–32°C.

Jumps occurred in a chamber of optical quality glass 80 mm wide, 80 mm tall and 25 mm deep that had a floor of high-density foam. The jumps were spontaneous or were encouraged by an abrupt sound created by dropping from a height of 10 mm, a 1 mm thick piece of aluminium (weight 6 g) that formed the roof of the chamber. A pygmy mole cricket could jump in any direction relative to the camera (see supplementary material Movies 1–3) but the constraints of the arena ensured that most jumps were in the image plane of the camera. All analyses of the kinematics are based on the two-dimensional images provided by the single camera. Measurements of changes in joint angles and distances moved were made from jumps that were parallel to the image plane of the camera or as close as possible to this plane. Jumps that deviate to either side of the image plane of the camera by  $\pm 30$  deg were calculated to result in a maximum error of 10% in the measurements of joint or body angles. Selected images were analysed with Motionscope camera software (Redlake Imaging, San Diego, CA, USA) or with Canvas X (ACD Systems of America, Miami, FL, USA). To allow comparison of different jumps, the times were recorded at which the hind legs first moved and then lost contact with the ground (designated as time  $t=0$  ms, the time of take-off). The period between these two measurements defined the time over which the

body was accelerated in a jump. The weights of the insects were determined before images of their jumping performance were captured. Measurements are given as means  $\pm$  standard error of the mean unless otherwise stated.

The anatomy of the hind legs and metathorax was examined in intact insects and in those preserved in 70% alcohol or 50% glycerol. Specimens for scanning electron microscopy (SEM) were dried in a Balzers critical point drier (model CPD 020, Balzers, Liechtenstein), sputter-coated with gold/palladium alloy to a thickness of 10 Å and examined under a Leica Leo S440 analytical SEM (Cambridge, UK).

## RESULTS

### Ecology of pygmy mole crickets

*Xya capensis* were found in saturated soils in a variety of habitats. They were diurnal, spending much time basking above ground, occasionally rotating each of the hind legs rhythmically about the coxal joints, feeding and excavating burrows. Construction of a burrow involved digging with the front legs, head and pronotum to move the mud or wet sand initially downwards and then horizontally. The tunnels had a fragile roofing of mud pellets that were first masticated, before being flicked rapidly above the head and stuck to the roof. The resulting unbranched, horizontal tunnels had an average diameter of  $0.92 \pm 0.078$  mm (s.d.,  $N=7$ ) and were 80–120 mm long. The pygmy mole crickets lived in colonies, with their burrows spaced on average  $75 \pm 21.7$  mm (s.d.,  $N=32$ ) from one another. Typically a single pygmy mole cricket was found in each burrow but sometimes more than one individual was recovered, perhaps as a result of them moving into the nearest burrow when disturbed.

The habitat of the pygmy mole crickets was shared by tiger beetles (*Lophyra capensis*, *Habrodera* sp., *Platychile pallida*, Cicindellidae), the larvae of which inhabited vertical burrows [mean depth  $91.3 \pm 22.3$  mm (s.d.,  $N=8$ ) that were spaced on average of  $7.6 \pm 5.4$  per square metre (s.d.,  $N=10$  quadrats, range 2–21)] among the burrows of the pygmy mole crickets. The larvae of the tiger beetles are voracious predators and feed on a variety of arthropods including pygmy mole crickets that pass within reach.

When disturbed while above ground, pygmy mole crickets jumped powerfully or retreated to the nearest burrow, showing no preference for their own burrow under these circumstances. Where there were no burrows present, the pygmy mole crickets hid in small cracks in the soil or in furled leaves.

### Body form

An adult pygmy mole cricket has an elongated and thin body (Fig. 1A) that weighs  $8.3 \pm 0.07$  mg ( $N=20$ ) and measures  $5.6 \pm 0.12$  mm ( $N=20$ ) in length. The adults have rudimentary tegmina and reduced, membranous hind wings so that flight is not possible. The pronotum is prominent and is hinged with the more posterior part of the thorax. The tip of the abdomen has conspicuous paired cerci and paraprocts, each with arrays of long, fine hairs. The front legs are not enlarged as in true mole crickets (Grylloidea) but are similar in shape, although smaller, than the middle legs. The body is dominated by the enormous femora of the hind legs, which when the insect is viewed from the side, almost obscure the abdomen (Fig. 1A). The structure of the hind legs is distinct from that of the front and middle legs (Fig. 1B; Figs 2 and 3).

### Structure of the hind legs

The hind legs are  $6.8 \pm 0.01$  mm long ( $N=7$ ), the middle legs  $3.2 \pm 0.06$  mm ( $N=20$ ) and the front legs  $1.5 \pm 0.09$  mm ( $N=7$ ), giving a ratio of leg lengths relative to the front legs of 1:2.1:4.5

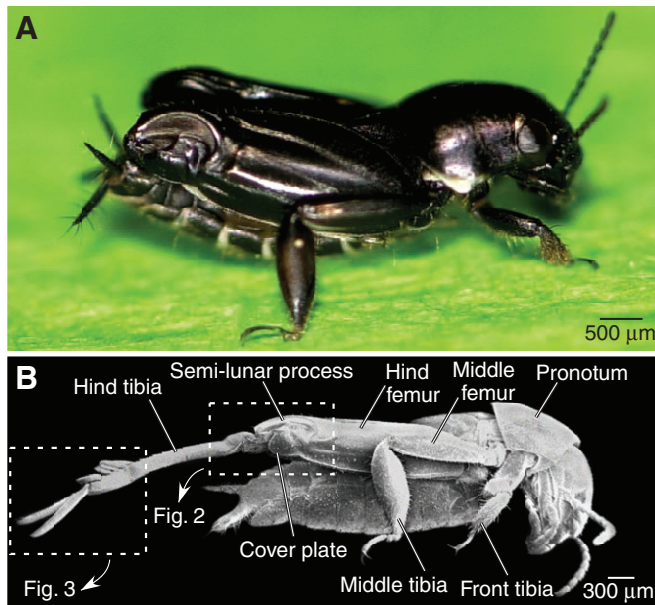


Fig. 1. Body structure of the pygmy mole cricket *Xya capensis*. (A) Photograph taken from the side with the right hind leg fully flexed and held off the ground. (B) Scanning electron micrograph of the whole body viewed from the side with the right hind leg fully extended. The regions outlined with the dashed boxes are shown in more detail in Figs 2 and 3.

(front:middle:hind, respectively). The femur of a hind leg is  $3.1 \pm 0.05$  mm long ( $N=7$ ) or more than twice as long as the middle femur ( $1.4 \pm 0.04$  mm,  $N=7$ ) and 5 times longer than the front femur ( $0.6 \pm 0.05$  mm,  $N=7$ ). At its widest point a hind femur measures  $1 \pm 0.03$  mm ( $N=7$ ) and is three times broader than the femora of the other legs. Overall the hind legs are  $131 \pm 2.2\%$  ( $N=7$ ) the length of the body and have a ratio of 3.6 relative to the cube root of the body mass (Table 1). The surfaces of the femora and tibiae are described as dorsal, ventral, medial and lateral with reference to their position when the tibiae are fully extended.

### Femur

A hind femur, unlike a front or middle femur, is grooved deeply along all its ventral surface to allow the tibia to be closely apposed to it when fully flexed. In this position, the tibia is hidden by the lateral edge of the femur when viewed from the side. At its double pivot joint with the tibia, the distal hind femur is dominated by paired semi-lunar processes on both its lateral (Fig. 1A; Fig. 2A) and medial sides. Each of these curved processes is made of heavily sclerotised, hard cuticle and is some  $900 \mu\text{m}$  long and  $250 \mu\text{m}$  wide. Its convex surface forms the distal end of the femur. Just ventral to a lateral semi-lunar process, the lateral wall of the femur is notched with a >-shaped cleft that has soft membrane at its proximal end (Fig. 2A). In locusts, this notch is closed when the extensor tibiae muscle contracts and the semi-lunar process bends to store energy in preparation for a jump (Burrows and Morris, 2001). Still further ventral, both the medial and lateral walls of the femur form thin cuticular cover plates (Fig. 1B; Fig. 2A,B) that enclose the flexible membrane of the femoro-tibial joint. The lateral cover plate is much larger than the medial one (Fig. 2B). This overall structure of the femur suggests that the joint may be distorted when the extensor tibiae muscle contracts and the tibia is fully flexed about the femur, in much the same way as happens in locusts (Bennet-Clark, 1975;

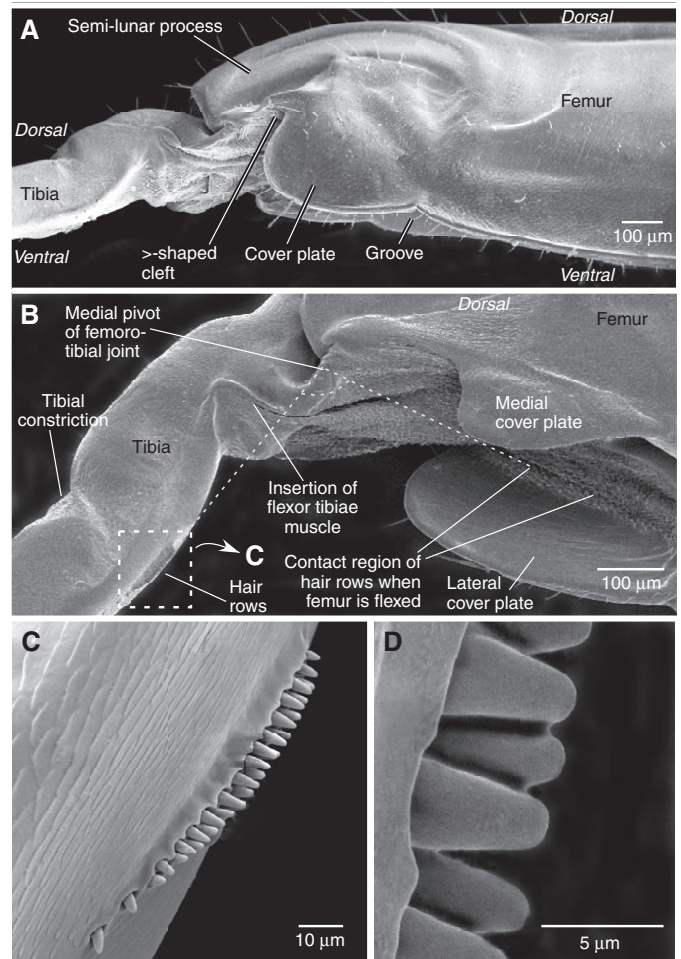


Fig. 2. Scanning electron micrographs of the femoro-tibial joint of a hind leg. (A) Lateral view of a right hind leg. The semi-lunar process is prominent on the dorsal distal edge of the femur and the lateral cover plate forms the distal ventral edge. The tibia is fully extended. Proximally it has a clear indentation on its ventral surface and a constriction on its dorsal surface. (B) A left hind leg viewed medially and rotated so that the ventral membranous part of the femur is visible between the two cover plates. Hair rows (the dashed box indicates the area enlarged in C) protrude from the inside (ventral) surface of the tibia on the opposite edge to the constriction. They will engage with the flexible femoral cuticle (indicated by the dashed lines extending from the pivot) when the tibia is fully flexed about the femur. (C) The hair rows at higher magnification. (D) Individual hairs (setae) at still higher magnification.

Burrows and Morris, 2001). The femur does not have a prominent internal protrusion, as in a locust (Heitler, 1974), that alters the lever arm of the flexor muscle as the femoro-tibial joint rotates. Similarly there is no pocket in the flexor tendon that could act as a lock to restrain the force of the larger extensor tibiae muscle during co-contractions that might precede a jump.

### Tibia

A hind tibia is  $2.7 \pm 0.07$  mm long ( $N=7$ ) and is therefore 13% shorter than a hind femur. It is nevertheless twice as long as a middle tibia and more than 5 times longer than a front tibia. It is a thin, tubular structure  $200 \mu\text{m}$  wide at its proximal end, tapering to  $125 \mu\text{m}$  distally. The extensor tibiae muscle inserts on the dorsal and most proximal edge of the tibia and the flexor tibiae muscle on the

Table 1. Body form of pygmy mole crickets *Xya capensis*

	Average (N=7)	Ratios
Front leg length (mm)		
Femur	0.6±0.05	
Tibia	0.5±0.03	
Tarsus	0.4±0.05	
Total	1.5±0.09	1
Middle leg length (mm)		
Femur	1.4±0.04	
Tibia	1.2±0.03	
Tarsus	0.5±0.03	
Total	3.2±0.06	2.1
Hind leg length (mm)		
Femur	3.1±0.05	
Tibia	2.7±0.07	
Spurs	1.1±0.04	
Total	6.8±0.1	4.5
Body length (mm)	5.6±0.12 (N=20)	
Body weight (mg)	8.3±0.07 (N=20)	
Front leg as % body length	29±0.07	
Middle leg as % body length	61±0.07	
Hind leg as % body length	131±2.2	
Normalised hind leg length (mm)/weight (mg) <sup>0.33</sup>	3.6	

proximal edge of an indentation of the ventral surface (Fig. 2B). Just distal to this, the dorsal surface is constricted in a plane that allows the tibia to bend. On the ventral surface at this plane of

weakness are two parallel hair rows about 115 µm long and consisting of a total of 29–36 hairs (N=4) (Fig. 2C,D). These rows stand proud of the ventral cuticle on a ridge with the hairs of each row interdigitating and closely apposed to each other along most of the length. At either end the rows taper to a few more widely space individual hairs. The hairs are each 5–6 µm long and 3.5 µm wide at their base (Fig. 2D). When the tibia flexes about the femur they will be pressed against the cuticular membrane between the two cover plates (Fig. 2B).

The structure of the distal end of the tibia is distinct from that of the other legs in having two pairs of distal spurs (apical and sub-apical) that are longer than the reduced tarsus, and more proximally, two rows of expanded lamellae. Each lamella pivots with the ventral surface of the tibia (Fig. 3A,B).

The two sub-apical spurs are 80 µm wide and 300–320 µm long (Fig. 3A–C). They pivot with the ventral distal end of the tibia, 150–180 µm proximal to the pivot of the long spurs. They can move through an angle of some 90 deg parallel with the long axis of the tibia and can also rotate around this articulation so that the medial one extends medially and the lateral one laterally. The tips of these short spurs are blunter than the longer spurs and are deeply indented on their ventral surface to form a terminal hook.

The two apical spurs are 100 µm wide and 840 µm long or 70% of the length of the tibia (Fig. 1; Fig. 3A,B). They are grooved on their ventral surface and end in a blunt tip with three hairs 75–100 µm long on their medial surface (Fig. 3D). These long spurs pivot about the distal end of the tibia and can rotate through an

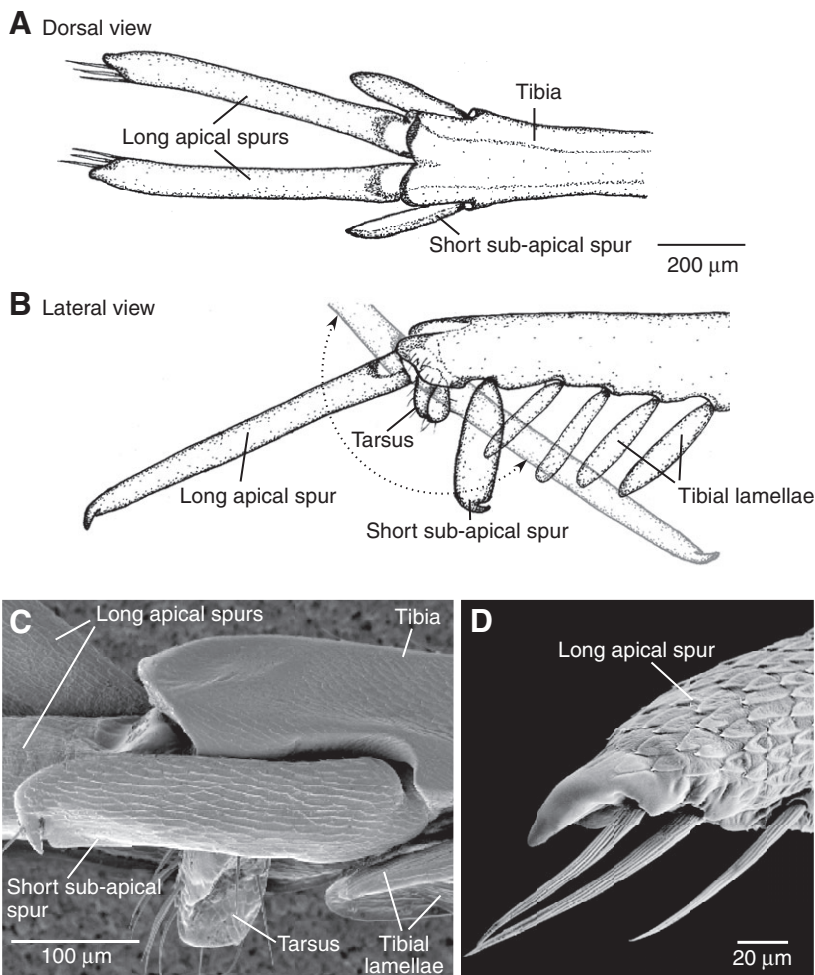


Fig. 3. Articulation of the tibial spurs. (A,B) Drawings of the pairs of long apical and short sub-apical spurs at the distal end of the tibia. A is a dorsal view. B is a lateral view to show a long spur at its mid position and at its two extremes (grey). The four lateral tibial lamellae are shown splayed out. The reduced tarsus protrudes ventrally between the spurs. (C) Scanning electron micrograph to show the articulation of a short spur with the lateral distal tibia. The tip of this spur is indented near its tip to form a point directed laterally. (D) The tip of a long spur has a group of three prominent and stiff hairs.

angle of 180 deg, being restrained by the notched end of the tibia at the extremes of their excursion. The plane of rotation is the same as that of the femoro-tibial joint and because the hind legs are held parallel to the long axis of the body, the long spurs will point directly forwards or directly backwards at their two extreme positions. The two long spurs can also be closely apposed to each other along their length or they can be splayed out in a V-shaped arrangement.

### Tarsus

The hind tarsi are only 100–115  $\mu\text{m}$  long and are almost obscured by the tibial spurs, emerging ventrally between them as a small pad with an array of some 10 dorsal hairs 70–80  $\mu\text{m}$  long and a few ventral hairs of similar lengths (Fig. 3C). They are 8 times shorter than the long, apical spurs and 3 times shorter than the short sub-apical spurs. Their role appears largely to have been supplanted by the long, apical spurs, particularly in jumping. They differ substantially in structure from the two-segmented tarsi of the front and middle legs (Fig. 1).

### Kinematics of the jump

The key movements in powering a jump were the rapid extensions of the tibiae about the femora of both hind legs (Fig. 4; and supplementary material Movies 1 and 2). The positions of six points

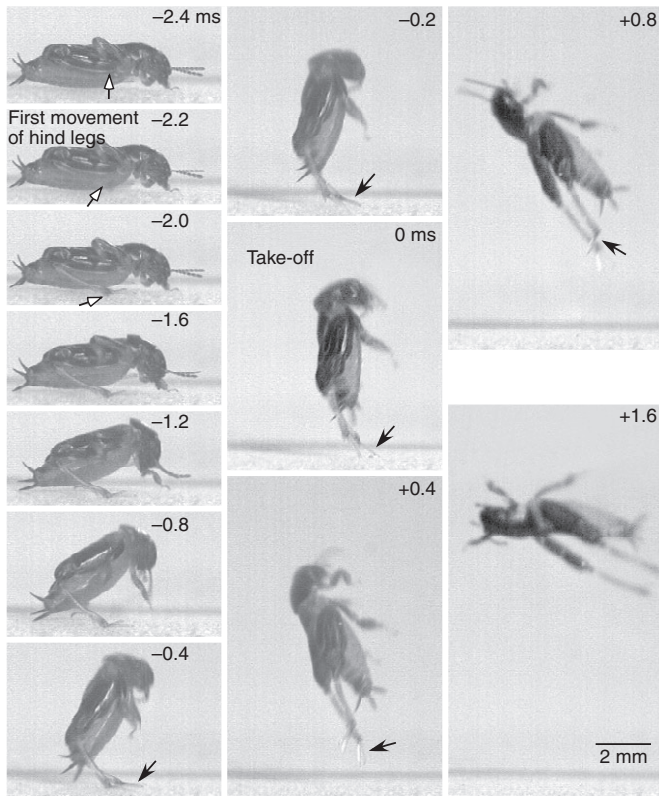


Fig. 4. Images of a jump viewed from the side and captured at  $5000\text{ s}^{-1}$  and each with an exposure time of 0.03 ms. The images are arranged in three columns with the bottom left-hand corner of each image providing a constant reference point. The hind tibiae (white arrows) were initially held off the ground ( $-2.4\text{ ms}$ ), started to move at  $-2.2\text{ ms}$  and hit the ground at  $-2.0\text{ ms}$ . The tibial spurs (black arrows) initially pointed forwards (e.g.  $-0.4\text{ ms}$ ), then rotated backwards toward take-off ( $-0.2\text{ ms}$ ), and after take-off had rotated through 180 deg so that they pointed backwards ( $+0.8\text{ ms}$ ). At take-off the body was almost perpendicular to the ground. Once airborne the body rotated backwards about its transverse axis.

on the body were plotted for two jumps from the horizontal to show the horizontal and vertical components of the movements (Fig. 5A,C) and the vertical movements against time (Fig. 5B,D).

Before a jump the hind tibia was held fully flexed about the femur and the tibial spurs pointed forwards so that the ventral edge of the tibia was some 500  $\mu\text{m}$  clear of the ground. This was the position in which the hind legs were normally held as pygmy mole crickets walked, propelled by the front and middle pairs of legs. There was therefore no overt movement of the hind legs that marked a period of preparation for a jump similar to that seen in locusts when the tibia is pulled into a fully flexed position about the femur (Heitler and Burrows, 1977), or in froghoppers when the hind trochantera are levated forwards and locked into their cocked position (Burrows, 2003; Burrows, 2006). A pygmy mole cricket made some adjustments to the angle of its hind femora relative to the body by rotation of the hind legs at the thoraco-coxal joints.

The first overt movement of a hind leg that preceded a jump was the rapid extension of the tibia, which propelled its tip and the long tibial spurs against the ground (Fig. 4; Fig. 5B,D) with a distinctive, audible thwack. In the 0.2 ms that it took for completion of this movement, the tibia moved at an angular velocity of  $100,000\text{ deg s}^{-1}$ . The continuing extension of the two hind tibiae pushed the tibial spurs against the ground so that they splayed out and pointed forwards (Fig. 4). The front and middle legs were also progressively raised so that only the hind legs remained in contact with the ground for the last 1.4–1 ms before take-off (Fig. 4; Fig. 5B,D). Take-off was measured as the time when the tips of the long tibial spurs lost contact with the ground. In the frame preceding this event, the tip of tibiae lost contact with the ground leaving only the tips of the long spurs touching the ground. From the first contact of the tibia with the ground until take-off (Fig. 4) the tibia was moved at an average angular velocity of  $68,000\text{ deg s}^{-1}$ . After take-off the long tibial spurs moved progressively backwards so that 1 ms later they now pointed posteriorly at right angles to the tibia and thus had moved through 180 deg from their position before the jump.

### Rotation of the head

As the hind legs applied force to the metathorax to accelerate the body, the head and the pronotum were jerked rapidly (Fig. 6; and Movie 3 in supplementary material). The force of the body movements also deflected the antennae downwards and backwards from their original forward-pointing direction. The movement of the head relative to the body began when the tibiae first made contact with the ground (Fig. 6A,B). During the continuing extension of the tibiae and before take-off was achieved, the head rotated downwards (Fig. 6A,C) about the thorax at an average rate of  $64,000\text{ deg s}^{-1}$ . At the same time the body rotated backwards relative to the ground at an average rate of  $43,000\text{ deg s}^{-1}$ , so that relative to the ground the head rotated at a rate of  $21,000\text{ deg s}^{-1}$ . The head reached its greatest excursion relative to the body 0.8 ms before take-off and then began to return to its natural angle, which it reached about 1 ms after take-off.

### Synchrony and asynchrony in movements of the hind legs

Jumps by the same pygmy mole cricket could be produced by two different combinations of movements of the hind legs.

The first combination was that the movements of both could be synchronous with no difference between the onset of the movements detectable at a resolution of 0.2 ms given by the selected frame rate ( $5000\text{ s}^{-1}$ ) of the camera. The jumps illustrated in Figs 4 and 6 were of this type. Second, both hind legs could be extended asynchronously. The differences in timing of the movements could be as large as the 2–3 ms that it took the body to be accelerated in

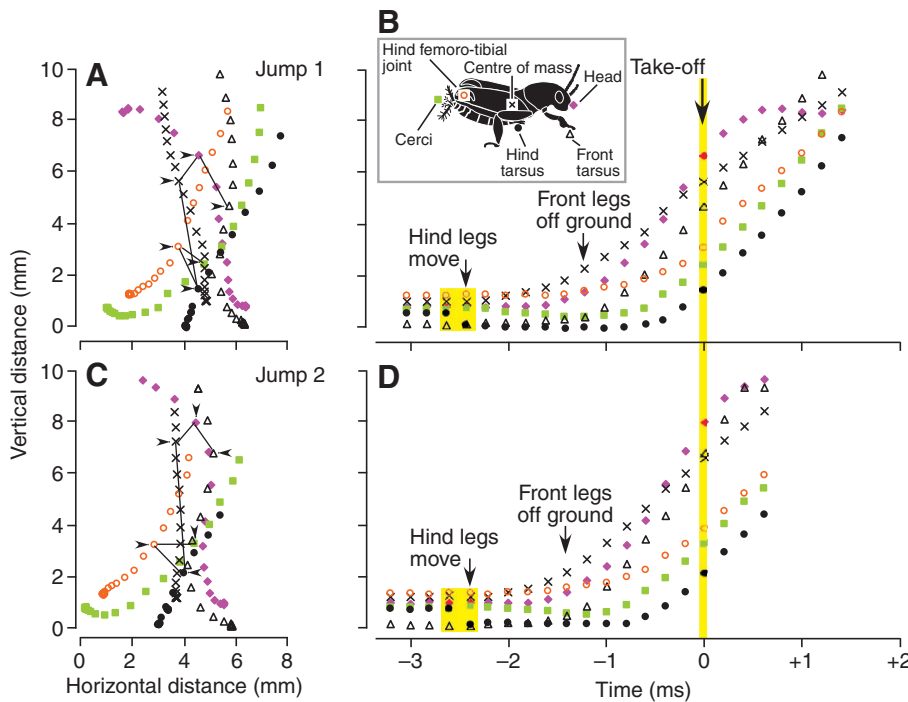


Fig. 5. Graphs of the positions of six points on the body (indicated in the cartoon) during two jumps (A,B) and (C,D) by the same *Xya capensis*. (A,C) The trajectory of the two jumps with vertical distance plotted against horizontal distance. The black arrowheads indicate the position of each body point at take-off. (B,D) Vertical distance is plotted against time. The first movement of a hind leg is apparent as downward movement of the tip of its tibia (yellow box). In both jumps the front and middle legs lost contact with the ground before take-off.

a jump. The longer the delay the further the first hind leg alone had raised the body from the ground with the consequence that the delayed hind leg was initially accelerated even more quickly because it did not bear the weight of the body. It therefore contacted the ground at even greater velocity. If the delay was such that one

hind leg had propelled the body to take-off, then when the other leg extended, it did not contact the ground at all and the high velocity of its movement resulted in an over-extension and consequent bending of the tibia at a constriction some 350  $\mu\text{m}$  distal to the pivot of the femoro-tibial joint (Fig. 2B).

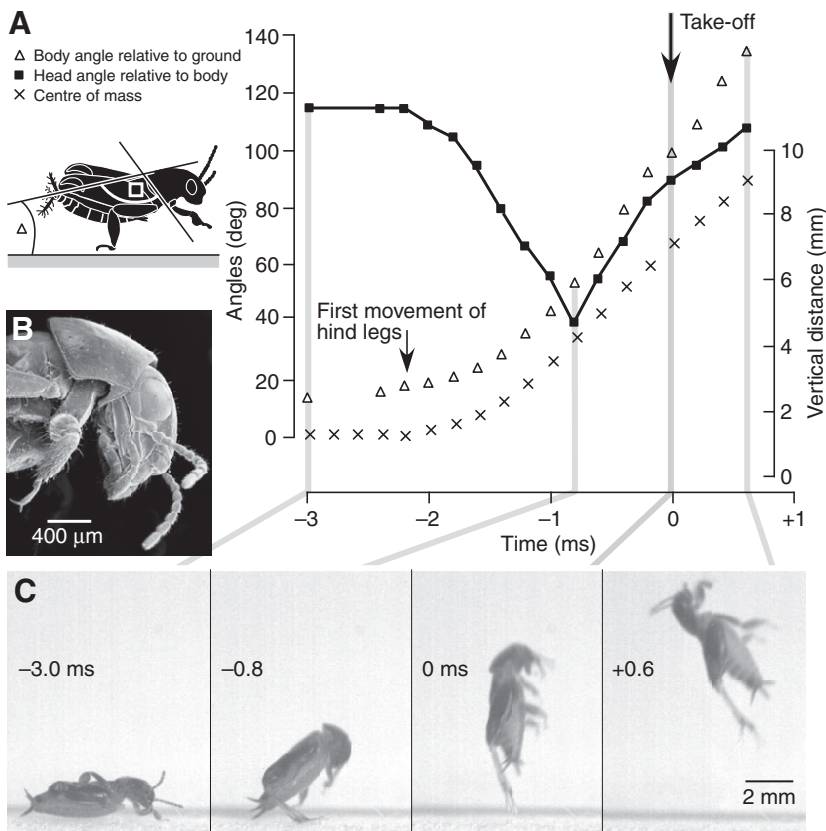


Fig. 6. Rapid movements of the head and pronotum during jumping. (A) Plot of the angular changes of the head and pronotum about the thorax during a jump and of the body relative to the ground. The trajectory of the approximate centre of mass (X) is plotted during the jump. The inset cartoon of *Xya capensis* shows the angles that were measured. (B) A scanning electron micrograph to show the head, pronotum and anterior thorax. (C) Selected frames from the jump at the times indicated to show the changing positions of the head, pronotum and body.

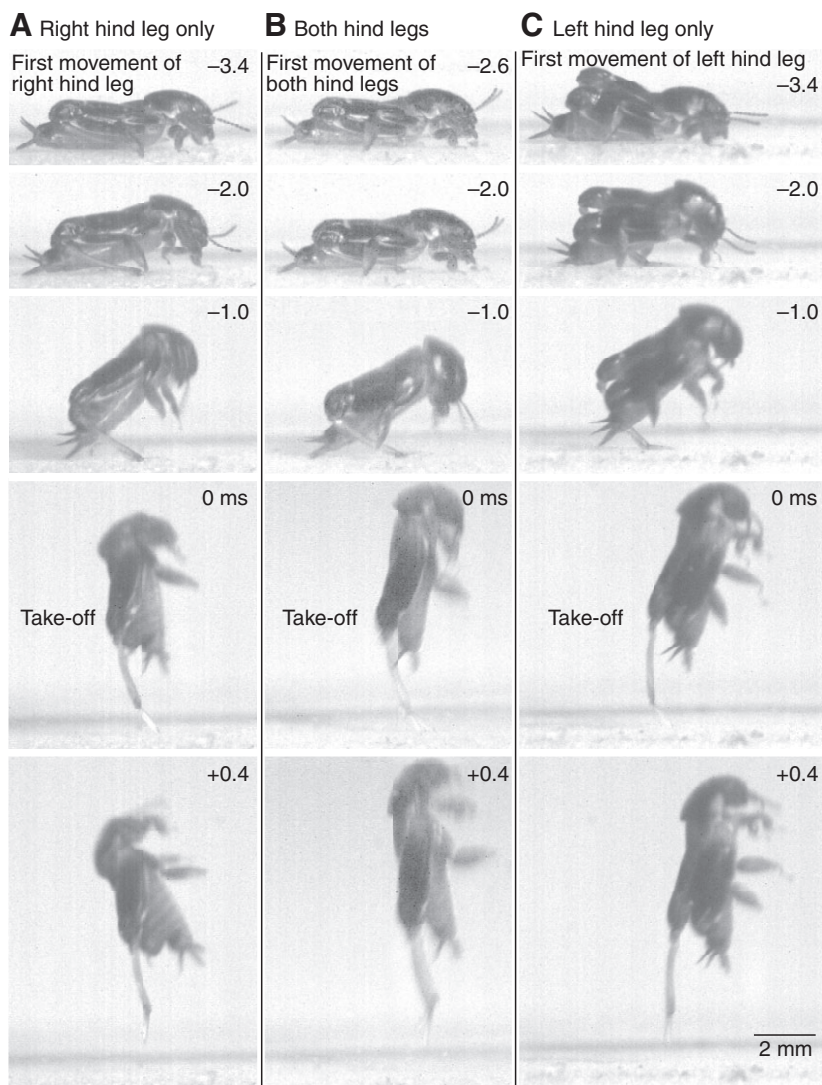


Fig. 7. One or both hind legs can propel jumping. (A–C) Three successive jumps by the same *Xya capensis*. (A) Jump in which only the right hind leg extended. (B) A jump in which both hind legs extended at the same time. (C) A jump in which only the left hind leg extended. The first movements of the hind legs of each jump are aligned in row 2, take-off in row 5 and 0.4 ms after take-off in the bottom row.

#### Jumps powered by one hind leg

Many jumps were powered by the movement of a single hind leg with the other hind leg remaining in its starting position with the tibia fully flexed about the femur (Fig. 7A–C). In 66 jumps by 15 *X. capensis*, 40 (61%) were powered by the movement of just one hind leg (Fig. 7A,C) and 26 (39%) used both hind legs (Fig. 7B). The same insect could jump with both legs or use either the left or the right hind leg alone in all possible combinations in a sequence of jumps. The use of just one hind leg had the following consequences for jumping performance.

When both hind legs were used the acceleration period of the jump averaged  $2.24 \pm 0.041$  ms (mean of means for 26 jumps by 15 *X. capensis*, range 1.8–2.6 ms). By contrast when just a single hind leg was used the period was significantly lengthened to an average of  $3.35 \pm 0.087$  ms (mean of mean for 40 jumps by the same 15 *X. capensis*, range 2.2–5.6 ms,  $t_{40,04} = 8.47$ ,  $P < 0.001$ ). If both hind legs were used, but the movement of one was delayed with respect to the other, the acceleration times were intermediate (3.2 ms,  $N = 4$  jumps by two animals).

The resulting take-off velocities were always lower when a single hind leg was used (Fig. 8). The mean take-off velocity when both hind legs were used was  $5.0 \pm 0.12$  m s<sup>-1</sup> (mean of means for seven animals, range 4.7–5.4 m s<sup>-1</sup>) (Fig. 8A) but when only one hind leg

was used the velocity fell significantly to  $3.2 \pm 0.17$  m s<sup>-1</sup> (mean of means for seven animals, range 2.7–3.6 m s<sup>-1</sup>,  $t_{9,02} = 9.05$ ,  $P < 0.001$ ) (Fig. 8B). The effects of these different velocities when using one or both legs were particularly apparent when comparing the time taken to reach a particular height in a jump. For example, a one-legged jump took 5.2 ms longer to reach a height of 30 mm compared with a jump by the same *X. capensis* that used both hind legs (Fig. 9A–D).

#### Trajectories

The take-off trajectories for jumps had a mean angle of  $84.3 \pm 3.82$  deg (mean of means for 27 jumps by seven animals, range 70–98 deg). The angle of the body relative to the ground at take-off was also high with a mean angle of  $85.0 \pm 3.53$  deg (mean of means for 25 jumps by seven animals, range 42–115 deg). Elevation of a jump appeared to depend on the angle of the hind femur and tibia relative to the ground (before the start of tibial extension) that was set by rotation at the thoraco-coxal joint. A low angle of the hind legs relative to the ground appeared to result in a high angle of the body relative to the ground at take-off. The same apparent effect of the starting position of the hind legs on the body angle at take-off was seen when jumps were powered by the movements of a single hind leg or by both hind legs. However, when the angle of

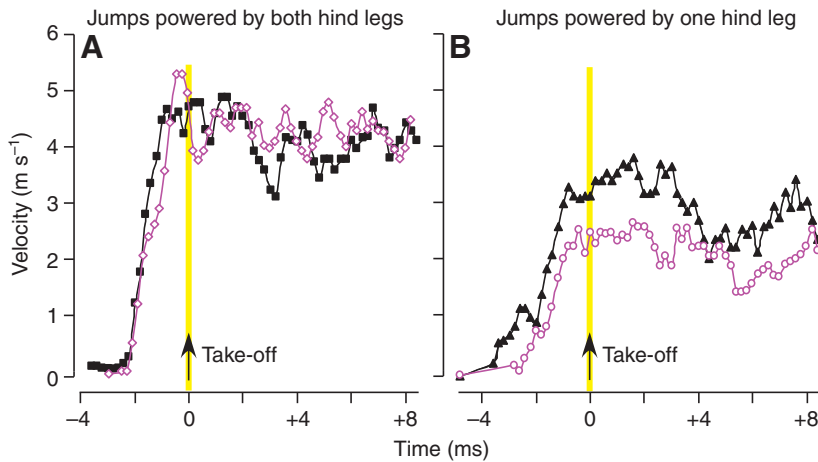


Fig. 8. Velocities of jumps powered by both hind legs (A) or by just one (B). Each of the two *Xya capensis* (one shown with black filled symbols and the other with open pink symbols) performed a jump powered by both hind legs and then a jump powered by one hind leg. Take-off velocities are plotted against time as rolling 3-point averages.

the hind legs at the start of a jump was plotted against the body angle at take-off, there was a weak negative correlation ( $R^2=0.368$ ). In an analysis of covariance (ANCOVA) that considered the jumps by 19 individuals, there was a significant difference between individuals ( $F_{17,33}=2.27$ ,  $P=0.021$ ) but the relationship between the

initial angle of the hind legs and the angle of the body relative to the ground at take-off just missed significance ( $F_{1,33}=4.77$ ,  $P=0.052$ ).

The trajectories in one- and two-legged jumps were similar and typically were dominated by a backwards rotation of the body about the transverse body axis (pitch plane) once airborne (Fig. 10). The rotation in this plane was high at 100–190 Hz in different jumps. By contrast, rotation in the yaw and roll planes was much less. Rotation in these planes could be measured directly when a jump was viewed head on or calculated when a jump was viewed from the side. For example, yaw was estimated from the apparent change in body length; 25 degrees of yaw will cause a 10% change in the body length. The only jump in which that much yaw was observed is in Fig. 7A, and this equates to a rotation rate of 50 Hz, which is much slower than the 189 Hz of rotation seen in the same jump in the pitch plane. Significant roll was not observed in jumping propelled by either one or both hind legs (e.g. Fig. 10). If the animal were to have rolled, this would have changed the orientation of the hind leg relative to the body but this is not observed. Nevertheless the spin in the pitch plane is dominant in both of these jumps.

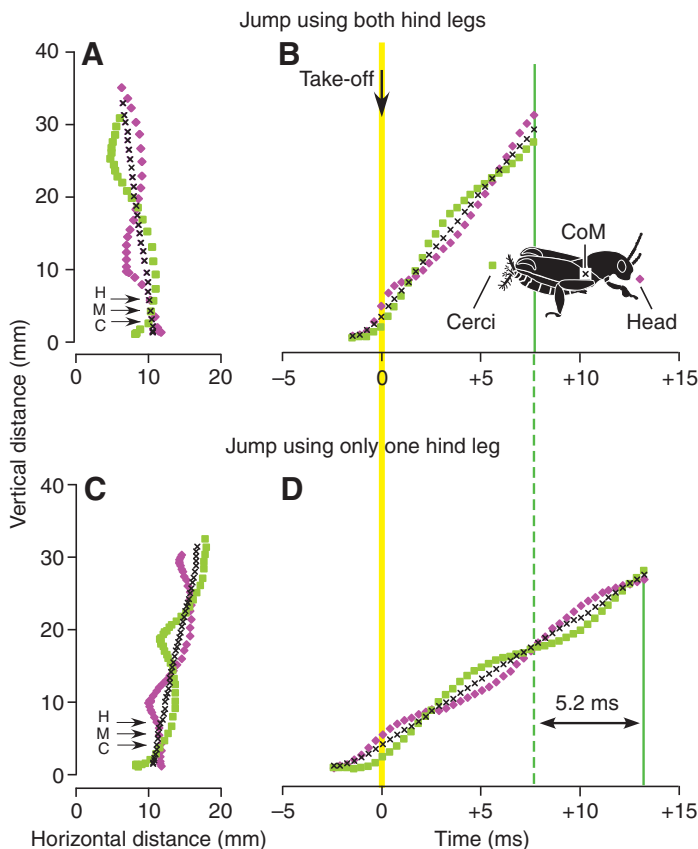


Fig. 9. Comparison of trajectories of successive jumps by the same *Xya capensis* powered by one or both hind legs. Three points on the body as indicated in the cartoon were plotted for each graph. (A,C) The trajectory of the two jumps with vertical distance plotted against horizontal distance. The black arrowheads indicate the position of each point at take-off. (B,D) Vertical distance is plotted against time. The time taken to reach the same vertical distance (green bars) is 5.2 ms longer when only one hind leg contributes. CoM, centre of mass. H, head. M, centre of mass. C, cerci.

### Jumping performance

The height and distance jumped from the vinyl floor of the laboratory were measured by two observers; one recording height against a calibrated background and the other the actual distance. In 97 jumps, the mean of the mean distance jumped by eight pygmy mole crickets was  $477 \pm 27$  mm, with the best jumps achieving 1420 mm or 250 times the body length. The mean height achieved was  $415 \pm 22$  mm, with the best jumps reaching 700 mm or 125 times its body length. The mean values are likely to under-represent the jumping performance because it was impossible to tell whether jumps were propelled by one or both of the hind legs.

Further features of the jumping performance were calculated from the data obtained from the high-speed images (Table 2). For jumps powered by movements of both hind legs, the average acceleration over the whole of the take-off period was  $2192 \pm 116.4$  m s<sup>-2</sup> ( $N=7$ ). The average acceleration rose to  $3000$  m s<sup>-2</sup> in the best jumps so that a pygmy mole cricket would have experienced forces of  $306g$ . The energy required to achieve these performances was on average  $116 \pm 15.1$   $\mu$ J, the power output was  $50 \pm 5.6$  mW and the force exerted was  $20 \pm 1.9$  mN. When the jumps were powered by a single hind leg these figures were about 40–50% of those when both hind legs were used. The acceleration fell to  $1043 \pm 47.4$  m s<sup>-2</sup> ( $N=7$ ) and in the best jumps was  $1636$  m s<sup>-2</sup> because the period during which the body was accelerated was longer. The energy required was



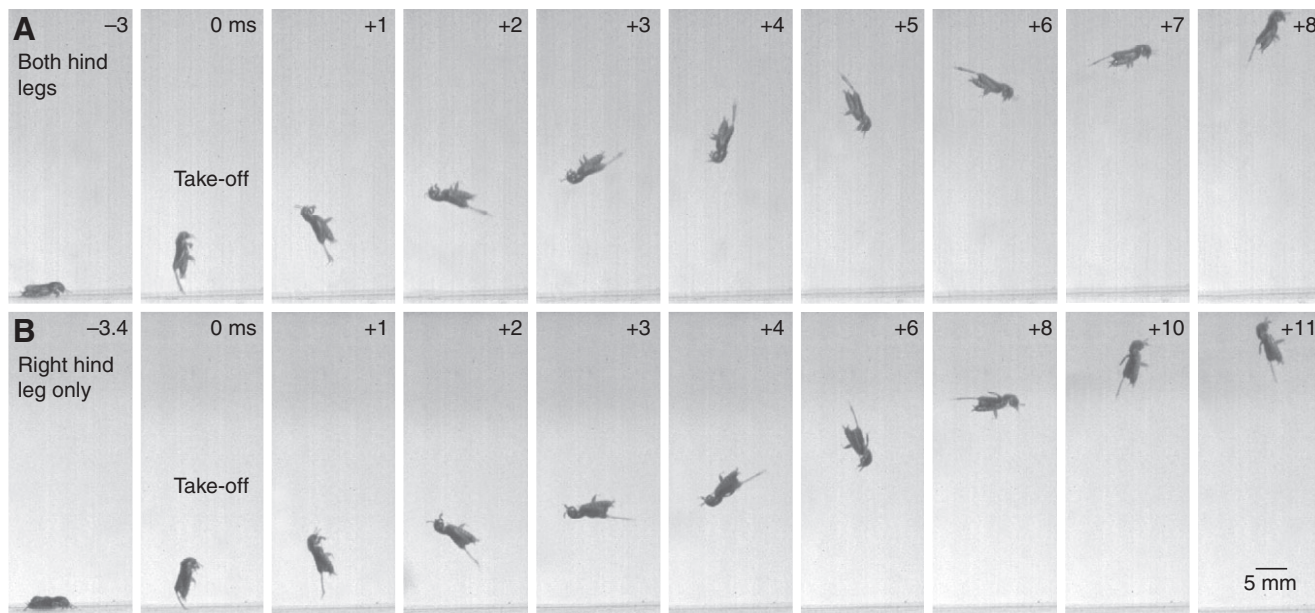


Fig. 10. Rotation of the body about the transverse body axis during jumping. (A) A jump powered by the movements of both hind legs in which the body rotates backwards. (B) A jump of the same *Xya capensis* powered by the movements of the right hind leg alone. Selected frames from the jumps at the times indicated are shown.

43±6.6 μJ, the power output was 14±1.8 mW and the force exerted was 9±0.7 mN.

**Walking**

The specialisations of the hind legs for jumping is emphasised by the fact that they did not contribute to walking on horizontal surfaces (Fig. 11). Instead the femora were held parallel to the long axis of the abdomen, which in turn was held close to the ground, and the tibiae were fully flexed so that they fitted tightly into the ventral grooves of the femora. The hind legs made no contact with the ground during any part of the stepping cycles of the other legs (Fig. 11A,B). Walking was therefore powered only by movements of the front and middle legs in a quadrupedal pattern in which each leg was lifted from the ground sequentially to execute its swing phase (Fig. 11B).

**DISCUSSION**

Jumping in pygmy mole crickets is powered by rapid extension of the hind tibiae as in other orthopteran insects. The body is accelerated to mean take-off velocities of 5 m s<sup>-1</sup> in 2.2 ms so that in the best jump a pygmy mole cricket will experience more than

300 g. The energy requirements calculated to be needed for a jump could not be met by direct contractions of the mass of muscle that could be contained with the femora, assuming normal properties of striated muscle. This indicates that a catapult mechanism must operate as in fleas (Bennet-Clark and Lucey, 1967), locusts (Bennet-Clark, 1975; Heitler and Burrows, 1977), froghoppers (Burrows, 2006), leafhoppers (Burrows, 2007) and planthoppers (Burrows, 2009). It follows therefore that the tibial extensor muscles must contract slowly, thereby distorting cuticular structures such as the semi-lunar processes to store energy, which is then released suddenly to extend the tibiae rapidly and accelerate the body to take-off. Because the hind legs are held with the tibiae off the ground before a jump is initiated, any manifestations of these contractions by the tibial muscles cannot be discerned from the high-speed images. The first detectable movements are the high velocity movements of the tibiae at angular rotations of 100,000 deg s<sup>-1</sup> before they contact the ground and then have to accelerate the body to take-off. These initial movements may have implications for the stability and targeting of a jump because it will be hard to control where the spurs are placed on the ground. Contact may therefore be with an uneven part of the ground, which

Table 2. Jumping performance of pygmy mole crickets *Xya capensis*

	Time to take-off (ms)	Take-off velocity (m s <sup>-1</sup> )	Weight (mg)	Acceleration (m s <sup>-2</sup> )	<b>g</b> force	Energy (μJ)	Power (mW)	Force (mN)
<i>Xya capensis</i> (N=20)			8.3±0.07					
Both hind legs								
Average (N=7)	2.24±0.041	5.0±0.12		2192±116.4	224±11.9	116±15.1	50±5.6	20±1.9
Best	1.8	5.4	8.5	3000	306	124	69	26
One hind leg								
Average (N=7)	3.35±0.087	3.2±0.17		1043±47.4	106±4.8	43±6.6	14±1.8	9±0.7
Best	2.2	3.6	8.3	1636	167	54	24	14

The average values given are the means of the means of 26 jumps propelled by both hind legs and 40 by one hind leg performed by seven pygmy mole crickets. Best jumps are defined by their take-off velocity.

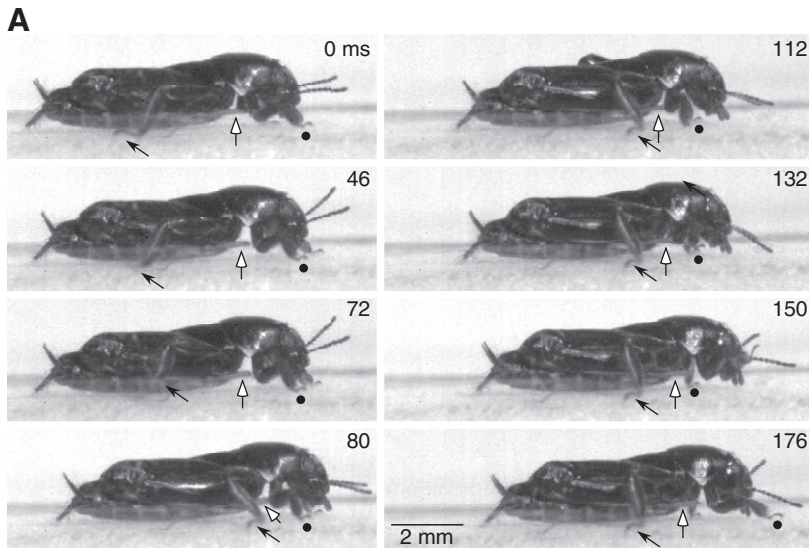
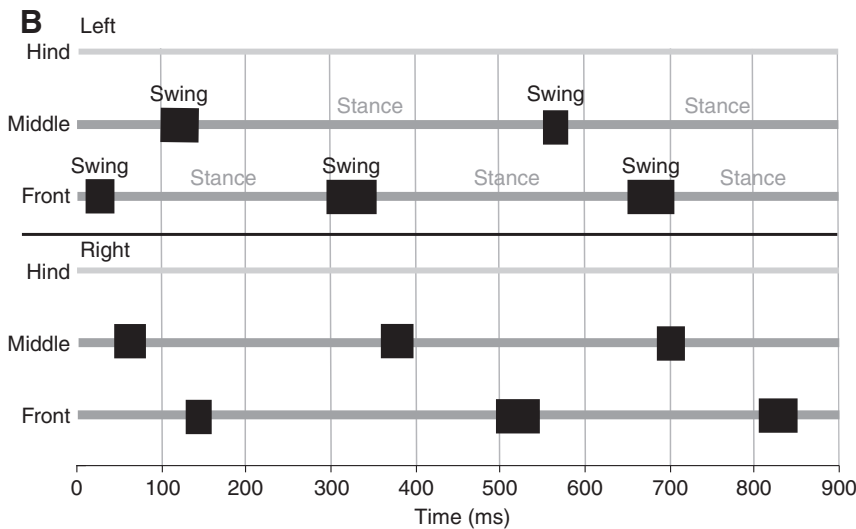


Fig. 11. Leg movements during horizontal walking. (A) Selected frames at the times indicated during walking. The vertical arrows with white heads indicate the position of the right hind tibia, the diagonal black arrows the start of the swing phase by the right middle leg, and the black circle the position of the right front tarsus. (B) The pattern of leg movements during two stepping cycles. The period when the front and middle legs were in contact with the ground (stance phase) is indicated by the thin grey bars, and the period when they were lifted from the ground and swung forwards relative to the body (swing phase) are indicated by the thick black bars. The immobile hind legs are indicated by thinner and lighter grey bars.



could result in differences in the timing and effectiveness of the forces applied by the two hind legs.

The high accelerations and the high velocities of a jump place huge constraints on the construction of the body, with the head being subjected to high accelerations, and the danger of over-extension of the tibiae being ever present. The head and pronotum must be well armoured to allow burrowing but may also serve a balancing function during jumping by buffering rotational momentum and possibly affecting the trajectory. The structural specialisations of the hind legs also show significant specialisations compared with other excellent orthopteran jumpers such as locusts and bush crickets.

**Design for jumping**

The hind legs of pygmy mole crickets are long relative to the other legs and to the body. They are 4.5 times longer than the front legs, more than twice as long as the middle legs (ratio, front:middle:hind legs of 1:2.1:4.5) and 31% longer than the body. By contrast, in locusts the hind legs are only 2.7 longer than the front legs (ratio, 1:1.2:2.7 for male, gregarious *S. gregaria*) and the same length as the body (Table 3). Similarly in male *P. teretrirostris* the ratio of leg lengths is 1:1:2.1, and relative to the elongated body the hind legs are only 77% of body length. In bush crickets, the hind legs are almost 3 times longer than the other legs (ratio of 1:1.1:2.9) but

relative to the body their long length becomes particularly striking; in male *P. griseoptera* they are twice as long as the body and in *Cederbergiana imperfecta* they are more than 3 times longer (M.B., unpublished observations).

The hind femur is very broad to accommodate the large extensor tibiae muscle that propels jumping. Two features of the femur are shared with locusts and would appear to be key to successful jumping. First, the ventral surface of a femur is grooved so that the tibia can be fully flexed while the extensor tibiae muscle contracts slowly to build up force. Second, semi-lunar processes are also a prominent feature of the distal femur. In locusts these are bent during the co-contraction of the flexor and extensor tibiae muscles and then unfurl rapidly once the tibiae starts to propel a jump thus delivering their stored energy (Bennet-Clark, 1975; Burrows and Morris, 2001).

The tibia has the same defining characteristics as in locusts of being a stiff, light lever that can be accelerated rapidly. It does, however, differ in two significant ways. First, the inner surface of the proximal tibia has rows of closely packed, short and stiff hairs that will be pressed against the ventral surface of the femur when the tibia is fully flexed. Both their structure and the contact they should make with the femur when the tibia is fully flexed suggests that they could act as a sense organ. They could provide information about the state of

Table 3. Comparison of the jumping performance of pygmy mole crickets *Xya capensis* (data in this paper) with some other jumping insects (data from other papers)

	Weight (mg)	Body length (mm)	Ratio of leg lengths			Hind leg as % body length	Hind leg length (mm)/ body mass <sup>0.33</sup> (mg)	Time to take-off (ms)	Take-off velocity (ms <sup>-1</sup> )	Acceleration (m s <sup>-2</sup> )	Energy (μJ)	Power (mW)
			Front	Middle	Hind							
Orthoptera												
<i>Xya capensis</i>	8.3	5.6	1	2.1	4.5	131	3.6	1.8	5.4	3000	124	69
<sup>1</sup> <i>Schistocerca gregaria</i>	1600	41.4	1	1.2	2.7	108	4.3	25-30	3.1	180	11000	333
– male												
<sup>2</sup> <i>Prosarthria teretirostris</i>	280	67.5	1	1	2.1	77	7.9	30	2.5	165	850	28
– male												
<sup>3</sup> <i>Pholidoptera griseocaptera</i>	415	21.6	1	1.1	2.9	181	5.1	30	1.5	83	490	16
– male												
Siphonaptera												
<sup>4</sup> <i>Archaeopsylla erinacei</i> (Hedgehog flea)	0.7	1.8	1	1.3	1.9	157	3.1					
<sup>5</sup> <i>Spilopsyllus cuniculus</i> (rabbit flea)	0.45	1.5						0.8	1.0	1330	0.2	0.3
Hemiptera												
<sup>6</sup> <i>Philaenus spumarius</i>	12.3	6.1	1	1	1.5	66	1.7	0.9	4.7	5400	136	155
<sup>7</sup> <i>Issus coleoptratus</i>	21.5	6.7	1	1	1.2	65	1.8	0.8	5.5	7051	303	388
– male												

<sup>1</sup>Bennet-Clark, 1975; <sup>2</sup>Burrows and Wolf, 2002; <sup>3</sup>Burrows and Morris, 2003; <sup>4</sup>G. P. Sutton and M.B., unpublished; <sup>5</sup>Bennet-Clark and Lucey, 1967; <sup>6</sup>Burrows, 2006; <sup>7</sup>Burrows, 2009.

flexion of the tibia about the femur and thus about the phase of jumping when muscular contractions are occurring and energy is being stored. Such a sense organ has not been described in other orthopterans or in other jumping insects which power jumping by extension of the hind tibiae. A similar structure to that described here has also been found on a fossil Tridactylidae from the early Eocene (Azar and Nel, 2008). The only comparable structure in a locust that will be stimulated when the hind tibia is fully flexed is a tubercle on the femur called Brunner's organ, the function of which is still unclear (Jellema and Heitler, 1997; Slifer and Uvarov, 1938).

The second structural difference of the tibia is the presence of two pairs of apical spurs, the largest of which are 70% of the length of the tibia and more than 8 times longer than the much reduced tarsi, the role of which they appear to subsume. The ventral surface of the spurs has no structures that could improve traction with the substrate as do the tarsi in most insects. Again a fossil Tridactylidae has these long spurs but a tarsus of the same length is present (Azar and Nel, 2008). The high-speed images of jumping show that these spurs are splayed out and point forwards as a tibia first contacts the ground. This positioning should distribute the load of the body over a wider surface area when only the hind legs are in contact with the ground before take-off. The spurs then rotate backwards so that at the point of take-off they are almost parallel with a tibia and are the last point of contact with the ground. Once airborne, the spurs rotate further so that they eventually point backwards having moved through some 180 deg. How are these spurs controlled? If they are to act as pivots for the jump, then there must be some resistance that allows transmission of the force for jumping. It is not known whether the movements of these spurs are under active muscular control. In other orthopterans, such as the locust, the equivalent but proportionately much shorter spurs can also rotate through small angles in their sockets but do not appear to be under direct control by specific bundles of muscle fibres. If, in pygmy mole crickets, they are not under muscular control and offer no substantive resistance, then the effective take-off time has to be considered to be at least 0.2 ms earlier (frame -0.2 ms instead of frame 0 ms in Fig. 4). Once airborne the spurs move toward their forward-pointing position. Are they spring-loaded and thus return to their default position? The control of these structures remains to be resolved.

During horizontal walking, the tibiae of the hind legs are kept fully flexed about the femora and rotated about the coxae so that they lie parallel with the abdomen. In this position they are not in contact with the ground and therefore do not contribute to walking. Locusts, grasshoppers and bush crickets all use their hind legs in walking and climbing although the regularity of their contribution to the alternating tripod gait in horizontal walking can be less than for the two other pairs of legs. The parallels between pygmy mole crickets and froghoppers are stronger, because in these insects the hind legs are also held in their cocked position during walking so that they do not contribute propulsive or stabilising forces (Burrows, 2006). Froghoppers do, however, appear to use their hind legs during manoeuvres such as vertical climbing. By contrast, there are no observations to suggest whether pygmy mole crickets use their hind legs in other behaviour but the narrowness of their burrows alone suggests they would be of little value underground and that therefore holding them parallel to the longitudinal axis of the body would be advantageous.

**Jumping performance**

A notable feature of the jumps of pygmy mole crickets are the take-off angles, which are much steeper than the 45 deg that would be

optimal for achieving the most effective translation of the body. Moreover, many of the jumps have trajectories that are close to vertical either in the forwards or even in the backwards direction. In these jumps in particular, the body rotates at initial velocities above 100 Hz about the transverse axis of the body, so that much energy must be lost to rotation instead of being translated into forward momentum. Nevertheless in their best jumps a pygmy mole cricket can be propelled forwards for almost 1.4 m or 250 times its body length (therefore matching the best performance of the planthopper *I. coleopratus*) and to a height 0.7 m or 125 times its body length (thus matching the performance of the frog hopper *P. spumarius*) (Burrows, 2003; Burrows, 2006). By comparison, other larger orthopterans such as a locust can only jump a forward distance of some 15 times its body length, a male *Prosarthria* or a male bush cricket *P. griseoptera* a little less.

Pygmy mole crickets accelerate more rapidly than do locusts, *Prosarthria* or bush crickets, and have higher take-off velocities in jumping (Table 3). For example, while it takes a pygmy mole cricket just 2 ms to reach  $5 \text{ m s}^{-1}$ , a locust takes 25–30 ms to accelerate its body to a take-off velocity of  $3.1 \text{ m s}^{-1}$ , *Prosarthria* takes 30 ms to reach  $2.5 \text{ m s}^{-1}$ , and a bush cricket *Pholidoptera* takes 30 ms to reach  $1.5 \text{ m s}^{-1}$ . A bush cricket generates its jump by direct contraction of the extensor tibiae muscles acting on long levers (Burrows and Morris, 2003) while all the other insects use a catapult mechanism. The differences in jump performances are also reflected in their energy requirements; a pygmy mole cricket requires 0.1 mJ, a bush cricket 0.5 mJ (Burrows and Morris, 2003), a *Prosarthria* 1 mJ (Burrows and Wolf, 2002) and a locust 10 mJ (Bennet-Clark, 1975).

The two hind legs did not always move synchronously when propelling a jump in pygmy mole crickets but instead could move with differences in timing as great as the acceleration period of a jump. In extreme examples the first leg to move had propelled the insect to take-off before the second hind leg started to move. A consequence was that the second hind leg did not bear the load of the body and as it extended at high rotational velocities did not touch the ground. The tibia was then over-extended by bending at the constriction zone in the proximal tibial, which absorbed the momentum which otherwise might have damaged the femoro-tibial joint. This structural adaptation suggests a solution to the problem created by asynchronous movements propelling jumping that is similar to the one adopted by locusts. A contrasting solution used by planthoppers is to ensure close synchrony between the movements of the hind legs by mechanical interactions between the hind trochantera (Burrows, 2010).

Detailed analysis of the high-speed images surprisingly showed that the majority of jumps were propelled by one hind leg, with a particular insect varying the particular hind leg used in successive jumps or using both hind legs synchronously. When only one hind leg was used the acceleration time rose from 2.2 ms to 3.4 ms and the take-off velocity fell from  $5 \text{ m s}^{-1}$  to  $3.2 \text{ m s}^{-1}$ . This means that not only did it take longer to take-off but it also took longer to reach the same vertical height in a jump propelled by just one leg compared with a jump of the same insect propelled by both hind legs. The trade-off for the pygmy mole cricket is that it would save on the energy expended.

Jumps propelled by asynchronous movements of both hind legs or by just a single hind leg did not rotate about the longitudinal axis of the body (yaw plane) although they still rotated about the transverse body axis (pitch plane). The reason lies in the orientation of the hind legs and their movement in different but parallel planes. The pygmy mole crickets thus conform to the same principle as in

locusts (Sutton and Burrows, 2008) but propel many more of their jumps with just one hind leg. Their performance, however, contrasts with that of frog hoppers (Sutton and Burrows, 2010) in which the movement of the two hind legs has to be very closely synchronised to produce effective jumps. If frog hoppers use just one hind leg they spin rapidly in the yaw plane and are unable to jump effectively.

### Biology of the jump

The most likely explanation for the remarkable jumping adaptations and performance of pygmy mole crickets may be the avoidance of predators such as sphecid wasps and tiger beetles and their larvae (Coleoptera, Cicindellidae). Two species of North American *Tachytes* wasps (Hymenoptera: Sphecidae, Larrinae) specialise on the pygmy mole cricket, *Neotridactylus apicalis* (Kurczewski, 1966). The crickets are dug out of their horizontal burrows and then immobilised with a sting, before being stored as provision for the larvae. Another sphecid wasp (*Lyroda*) also provisions its nests with pygmy mole crickets (Evans and Hook, 1984; Kurczewski and Spofford, 1985). The microhabitat favoured by Tridactylidae is also populated by tiger beetles, the larvae of which build their vertical burrows among those of the pygmy mole crickets. Both adult and larval tiger beetles are formidable, fast-moving predators. When basking and feeding outside their burrows, the pygmy mole crickets would inevitably be close to the burrows in which the larval beetles would be sitting and are also likely to encounter the adults. The exceptionally rapid and powerful escape response of the pygmy mole crickets may thus be a response to the constant threat thus posed. The large and heavily setose cerci and paraprocts may be associated with early detection of potential predators. Sound and vibration were an effective way of experimentally eliciting jumps.

Three features of jumping to emerge from this study point to its use primarily as an escape mechanism. First, an adult pygmy mole cricket lacks functional wings so that a jump cannot be to launch into flight. Furthermore, a jump cannot be stabilised or supplemented by forces generated by wings once the insect is airborne. Second, in insects like locusts which have hind legs that move in separate planes on either side of the body, the elevation of a jump is controlled by the angle of the hind legs that is set by rotation of the coxal joints. In locusts there is a good correlation between this angle and the take-off angle and hence the elevation achieved (Sutton and Burrows, 2008). By contrast in pygmy mole crickets, which have the same arrangement of their hind legs, this correlation just failed to reach significance, suggesting that setting elevation is subsidiary to other demands of jumping, such as speed. Third, many jumps by pygmy mole crickets result in rapid backward spinning of the body about the transverse axis and trajectories that are often backwards. All of these factors suggest that that the rapidity of take-off and the need to move as quickly as possible away from its current position take precedence. An advantage to such variable jumping as an escape mechanism is that predators cannot learn to predict the direction of a jump.

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