

## Jumping in a wingless stick insect, *Timema chumash* (Phasmatodea, Timematodea, Timematidae)

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### SUMMARY

The stick insect *Timema chumash* belongs to a sub-order of the phasmids that is thought to have diverged early from other stick insects, and which is restricted to the southwest of North America. It jumps by rapidly extending the tibiae of both its hind legs simultaneously from an initially fully flexed position, unlike any other stick insect that has been described. The hind legs are 1.5 times longer than the front and middle legs, but still represent only half the length of its body, and the femoro-tibial joints show few specialisations for jumping. In its best jumps, the wingless body is accelerated in 12 ms to a take-off velocity of  $0.9 \text{ m s}^{-1}$  and experiences an acceleration of  $75 \text{ m s}^{-2}$ , the equivalent of  $8 g$ . This performance requires an energy expenditure of  $19 \mu\text{J}$ , generates a power output of 1.6 mW and exerts a force of 3.6 mN. The jump propels the body forward a distance of 80 mm from a mean take-off angle of  $39^\circ$ . Heights of 20 mm were also achieved. Elevation of the jump was controlled by the initial position of the hind legs; when the hind tibiae and femora projected above the dorsal outline of the body the jump was forwards, when parallel with the long axis of the body the jump was backwards and could result in somersaulting. The jumping movements would appear to displace *Timema* in different directions away from a potential predator.

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Key words: kinematics, stick insect, locomotion.

### INTRODUCTION

Jumping has evolved many times in insects to become a major form of locomotion of particular species in many orders. The widespread occurrence of jumping, propelled by a variety of mechanisms, suggests it is an effective solution to a range of different behavioural demands. For example, jumping enables an insect to escape from a potential predator, to launch into flight, or to move most effectively from one place to another. Springtails (Collembola) jump by rapidly extending their terminal abdominal appendages (Brackenbury and Hunt, 1993) whereas some ants (Baroni et al., 1994; Tautz et al., 1994), a stick insect (Phasmida) (Burrows and Morris, 2002) and *Petrobius* (Thysanura) (Evans, 1975) use movements of the whole abdomen. By contrast, click beetles (Coleoptera) move the prothorax against the mesothorax (Evans, 1972; Evans, 1973) and the trap-jaw ant (Hymenoptera) rapidly closes its mandibles against the ground or an approaching object to propel itself upwards or backwards (Patek et al., 2006).

The most adept jumping insects, however, propel their jumps by rapid movements of the legs, with the hind legs typically specialised to provide most, if not all, of the power. The hind legs of many species are held alongside the body with the thrust for jumping generated by muscles moving the tibiae, as in locusts (Orthoptera) (Bennet-Clark, 1975; Godden, 1975; Heitler, 1977; Heitler and Burrows, 1977a; Heitler and Burrows, 1977b), bush crickets (Orthoptera) (Burrows and Morris, 2003) and flea beetles (Coleoptera) (Brackenbury and Wang, 1995), or the trochantera in fleas (Siphonaptera) (Bennet-Clark and Lucey, 1967; Rothschild and Schlein, 1975; Rothschild et al., 1975; Rothschild et al., 1972). In froghoppers (Burrows, 2003; Burrows, 2006a; Burrows, 2006b; Burrows, 2007c) and leafhoppers (Hemiptera) (Burrows, 2007a;

Burrows, 2007b) the hind legs are held underneath the body with thoracic muscles moving the trochantera. The propulsion can be generated by catapult mechanisms, as in locusts, fleas and froghoppers, in which energy from slow contractions of the muscles is stored, often in distortions of the cuticular skeleton and then suddenly released. An alternative strategy, as in bush crickets, is to have very long hind legs moved by direct contractions of the muscles acting on the long levers of the hind legs.

One order of insects in which jumping is uncommon is the Phasmatodea. The stick insects, or walking sticks, which belong to this group are usually characterised by their ability to merge into the background of the plants upon which they live and feed, due to their body shape and colouration. This camouflage is also aided by their behaviour, in particular by their ability to stay motionless for long periods – cataplexy (Bässler, 1983; Bässler and Foth, 1982; Bässler et al., 1982; Driesang and Büschges, 1993; Godden, 1974) – and by their slow and deliberate movements. Some stick insects are, however, faster moving and more pro-active in their responses to threats. In winged species, the wings can be flapped to power slow flight and when standing, may be raised to reveal patches of colour in apparent threat or startle responses that are accompanied by the generation of sound (Bedford, 1978; Bedford and Chinnick, 1966; Rehn, 1957). In only a few of approximately 3000 known species of stick insects (Bragg, 1995) do these responses grade into active escape movements (Robinson, 1968a; Robinson, 1968b; Robinson, 1969). One winged species that has been studied in detail, *Sipylloidea* sp. ‘Thailand 8’, throws the mass of its abdomen forward and pushes off the ground with its thin middle and hind legs in a jump that reaches a take-off velocity of between  $0.6$  and  $0.8 \text{ m s}^{-1}$  (Burrows and Morris, 2002). Another stick insect that belongs to a

sister group to the rest of the phasmids (Bradler, 1999; Kristensen, 1975; Tilgner et al., 1999) is also said to be able to jump. This sub-order (Timematodea) probably diverged early from the stock that gave rise to other phasmids (Vickery, 1993). It consists of a single genus with only a few species, which are small and flattened, and are restricted to altitudes over 850 m in the south-western USA (California, Nevada, Arizona) and northern Mexico. Only two of these species are widespread even within this region with the remainder, including the species studied here – *Timema chumash*, much more localised.

This study analyses the mechanisms that propel jumping in this species, determines the jumping performance and compares both with the jumping of other insects. It shows that *Timema* propels its jumps by rapidly extending the tibiae of its hind legs, which are short relative to its own body length. These movements propel the body to take-off velocities of  $0.9 \text{ m s}^{-1}$  upwards and forwards by several body lengths away from an approaching object, or following the appropriate orientation of the hind legs in a vertical or even a backward movement away from an apparent threat from in front.

### MATERIALS AND METHODS

*Timema chumash* Hebard, 1920 were collected by Greg Bartman from the San Gabriel Mountains in Los Angeles County, CA, USA. All the insects analysed were females; parthenogenesis is common in this genus (Sandoval et al., 1998). In the laboratory they were maintained at room temperature and fed on oak leaves (their normal host plants are *Ceanothus* or *Quercus*). They belong to the order Phasmatodea, sub-order Timematodea and to the family Timematidae. More widely known stick insects such as *Carausius* belong to sub-order Euphasmatodea and to the family Phasmatidae, and a species, *Sipyloidea* sp. Thailand 8 that also jumps to the family Heteronemiidae.

Images of jumping movements were captured with a high speed camera (Redlake Imaging, San Diego, CA, USA) at 1000 frames  $\text{s}^{-1}$  with an exposure time of 0.5 ms. The insects jumped in a chamber with a floor of high density foam and measuring 80 mm wide, 80 mm tall and 25 mm deep. Within these constraints, *Timema* could jump in any direction relative to the fixed position of the camera in front of the centre of the chamber. The insects were manoeuvred into position with a fine paint brush, but only five of the 49 jumps by six insects that were analysed followed directly upon contact of the brush with the insect and did not differ from the other jumps. Thirty five of the jumps were forwards and at right angles to the axis of the camera, four were backwards and in response to the brush approaching from the front, two were toward and five away from the camera. Two jumps were viewed from underneath as the insect jumped from the front wall of the chamber and one from above as it jumped from the back wall of the chamber. A high speed movie of a jump captured in this way is available as Movie 1 in supplementary material. Images were stored as computer files for later analysis with Motionscope camera software (Redlake Imaging), or with Canvas X (ACD Systems of America, Miami, FL, USA). The time at which the hind legs lost contact with the ground and the insect became airborne was designated as  $t=0$  ms so that different jumps could be aligned and compared. Detailed measurements of changes in joint angles and distances moved were made from jumps that were parallel to the image plane of the camera, or as close as possible to this plane. Calculations show that jumps that were up to  $\pm 30^\circ$  off the image plane of the camera would result in a maximum error of no more than 10% in the measurements of joint or body angles. These angles were not measured in jumps that deviated from this plane by more than  $30^\circ$ .

Photographs and anatomical drawings were made from both live and preserved specimens. Data are given as means  $\pm$  standard error of the mean (s.e.m.). All experiments were at room temperatures of 22–25°C.

## RESULTS

### Body shape

The six female *Timema chumash* used in this study had a body mass of  $47.5 \pm 7.3$  mg (mean  $\pm$  s.e.m.,  $N=6$ ) and a body length of  $12.0 \pm 0.68$  mm. Adult females of this species have a body length of about 24 mm (Vickery, 1993) suggesting that the ones used here were late stage instars. The body is green and with numerous pale raised spots (Fig. 1). Wings are not present in larvae or adults. The head is almost as broad as the pronotum and has antennae that are 60% of body length, often held pointing downwards (Fig. 1A). The breadth of the thorax is about 25% of body length and is about 50% greater than its dorsoventral height. The abdomen gradually tapers posteriorly.

All three pairs of legs emerge ventrally from the thorax (Fig. 1B) so that the coxae are not visible when viewed dorsally (Fig. 1C), a feature that contrasts with other stick insects. A further distinctive feature is that the tarsi of all the legs have only three articulated segments (articles) whereas other phasmids have five (Kevan, 1976). The front and middle pairs of legs project laterally from the body, whereas the hind legs are held more vertically and parallel with the long axis of the body so that the distal part of the hind femora and the proximal part of the tibiae alone project dorsally above the outline of the body (Fig. 1A). The hind legs were on average  $7.0 \pm 0.24$  mm long ( $N=6$ ), the middle legs  $4.9 \pm 0.12$  mm and the front legs  $4.8 \pm 0.08$  mm, so that the ratio of leg lengths was 1:1:1.5, front:middle:hind (Fig. 2B). The hind legs were, however, only  $57.02 \pm 3\%$  ( $N=6$ ) of the body length, but they were stouter than the other legs with the maximum width of the femur some 75% greater than that of the front or middle legs. The extensor tibiae and flexor tibiae muscles within the femur were of similar mass and each represented only 0.3% of total body mass.

The femoro-tibial joint of a hind leg consists of a double pivot that restricts movements of the tibia about the femur to one plane through an angle of about  $150^\circ$ . The extensor tibiae muscle has a

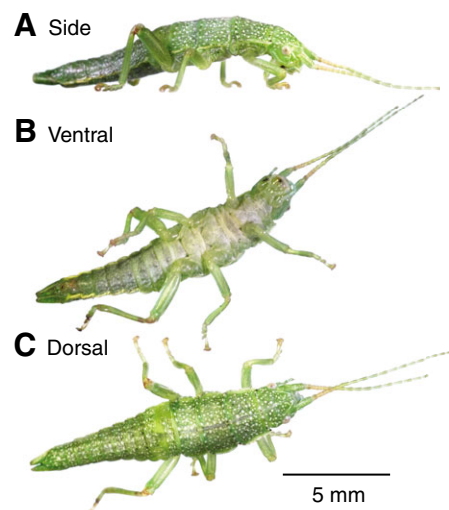


Fig. 1. Photographs of a female *Timema chumash* taken from the side (A), ventrally (B) and dorsally (C).

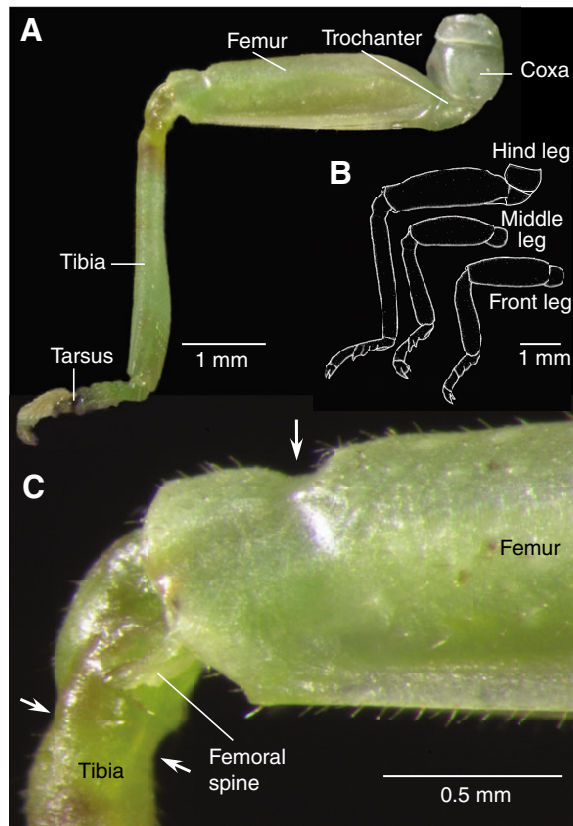


Fig. 2. Structure of the legs. (A) Photograph of a left hind leg viewed medially to show the relative proportions of the different segments. (B) Drawings of a hind, middle and front leg to show their relative sizes. (C) Photograph of the femoro-tibial joint of the right hind leg viewed laterally. The arrows indicate the constrictions in the distal femur and proximal tibia.

lever arm of about 16 when the femoro-tibial joint is at its mid position with an angle of  $90^\circ$ . The femur is indented dorsally just proximal to the articulation with the tibia and has a distally facing spine on both its lateral (Fig. 2A,C) and medial surfaces. It has no other specialisations that would apparently aid jumping. For example, it lacks semi-lunar processes at the femoro-tibial joint that provide an energy store in jumping by grasshoppers and locusts (Bennet-Clark, 1975). The tibia is cylindrical but widens somewhat towards its distal end. Proximally and close to the femoro-tibial joint is a constricted region (Fig. 2A,C) similar in location to the plane of weakness of a locust tibia and about which the tibia can bend (Heitler, 1977) when fully flexed against the femur and on the occasions when it is over-extended at the end of a jump or a kick.

### Jumping movements

Preparation for a forward jump began with a levation of the hind legs at their proximal joints so that the femora and tibiae projected above the dorsal outline of the body. The hind tibiae were fully flexed about the femora. The head was typically bent forwards so that both antennae pointed forwards and downwards to touch the ground in front of the head (Fig. 3A). The jump itself began with

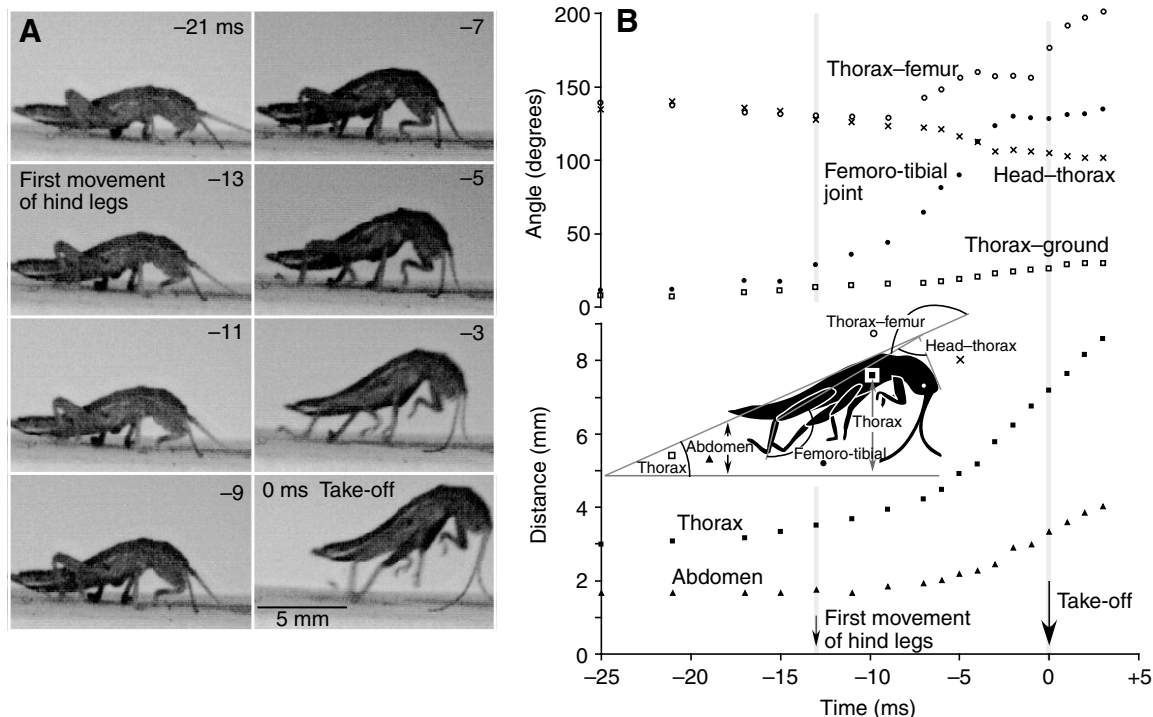


Fig. 3. Jump to the right captured with high speed imaging at  $1000 \text{ frames s}^{-1}$ . (A) Sequence of images from the jump at the times indicated. Take-off is achieved 13 ms after the first detectable movement of the hind legs. (B) Top graph shows angular changes of the right hind leg and the body during this jump. The four angles plotted and shown in the inset diagram are: femoro-tibial joint of the right hind leg (filled circles); the angle between the femur and the thorax (open circles), indicating the movement of the whole hind leg because the coxa and trochanter could not be resolved in these high speed images; the angle between the head and thorax (crosses); and the angle of the thorax relative to the ground (open squares). Bottom graph shows movements of the tip of the abdomen (triangles) and a point on the thorax during the same jump (filled squares).



the start of the extension of the hind tibiae about the femora  $14.9 \pm 0.28$  ms ( $N=46$ ; range 12–21 ms) before the hind tarsi left the ground and take-off was achieved (Fig. 3A,B). This period therefore

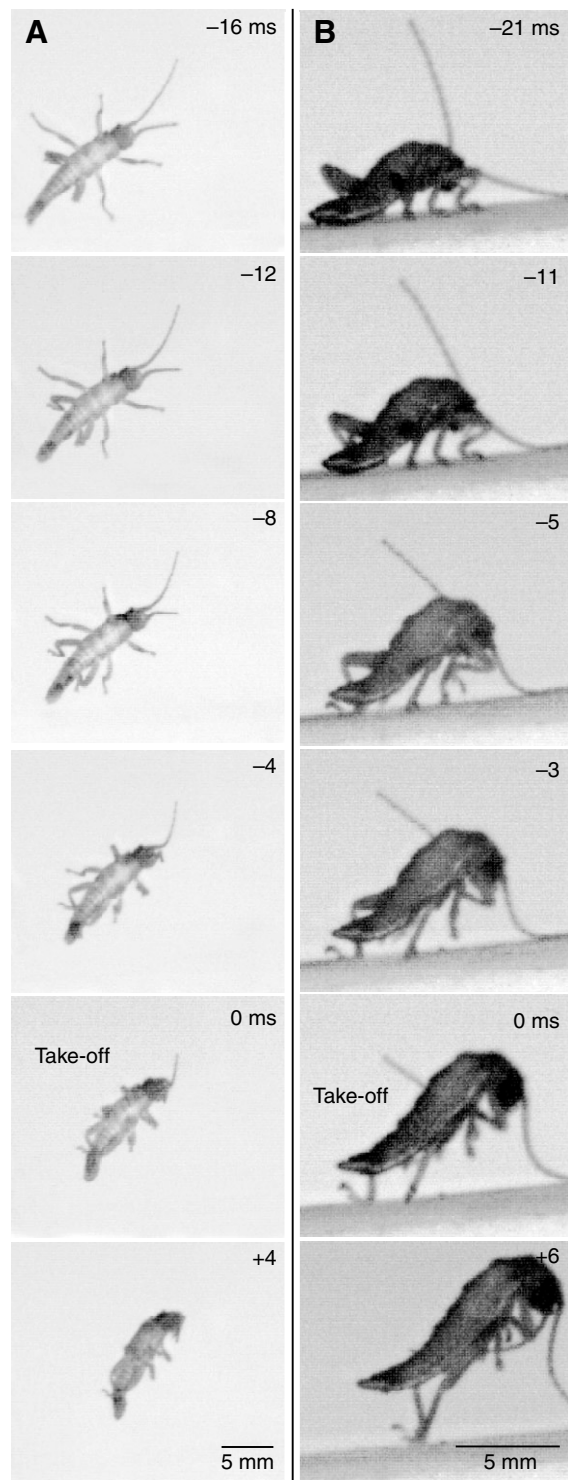


Fig. 4. Images from two jumps by two *Timema* at the times indicated and captured at  $1000 \text{ frames s}^{-1}$ . (A) A jump from the front wall viewed ventrally. The first movement of the hind legs occurred at  $-13$  ms before take-off. (B) A jump to the right and away from the camera viewed from behind. The first movements of the hind legs occurred at  $-12$  ms before take-off.

represents the time taken to accelerate the insect for jumping. In the best jumps that achieved the highest take-off velocities this period was only 12 ms, and conversely when the take-off velocity was slower, the period was longer. As the hind tibiae extended and the hind tarsi remained on the ground, the abdomen and thorax were gradually raised so that the front and middle legs lost contact with the ground (Fig. 3A). In some jumps both the front and middle pairs of legs were initially extended and may thus have contributed some early force to the jump. In all jumps, however, they lost contact with the ground before take-off and could thus not have contributed force to the later stages. The force applied to the metathorax by the rapid extension of the hind legs caused a whiplash-like movement of the head and pronotum. The angle between the head/pronotum and the thorax became more acute so that they pointed more directly downwards and this orientation continued throughout the later stages of the acceleration until take-off (Fig. 3). The antennae pointed directly downwards at take-off in part because of the more acute angle of the head with the thorax and because they were swept backwards by the force of the acceleration.

At the start of a jump viewed from underneath (Fig. 4A), both hind tibiae were fully flexed about the femora and held close to the lateral edges of the abdomen. The front and middle legs were splayed laterally with their femoro-tibial joints already extended. The result was that the hind tarsi were just below the lateral edges of the abdomen whereas the front and middle tarsi were more lateral. The first leg movements were the simultaneous extensions of the femoro-tibial joints of the hind legs that were not accompanied by similar movements of the other legs. In this particular jump therefore, the hind legs appeared to be the sole provider of power for the jump. The extension of the hind tibiae pushed the whole body forwards and resulted in the hind tarsi moving from their initial position just outside the lateral edges of the abdomen to one almost directly beneath the posterior tip of the abdomen just after take-off.

When viewed posteriorly so that a jump took the insect away from the camera, the dorsal and somewhat lateral projection of the hind legs at the start was particularly apparent (Fig. 4B). In this jump the right antenna pointed forwards and downwards to the ground and the left one was raised. The tibiae of the hind legs started to extend about the femora 12 ms before take-off and their continuing movement raised the body so that the front legs lost contact with the ground at  $-5$  ms and the middle legs at  $-3$  ms. The tibiae of neither the front or middle legs were extended about their femora during this acceleration period.

#### Jumping performance

To calculate the acceleration of the body and its trajectory during a jump, a point on the mesothorax was selected as being close to the centre of gravity in each *Timema*. This was confirmed by balancing a dead insect on a pin at this point. A rolling three point average of this part of the movement of the body showed that the peak of velocity was achieved about 2 ms before take-off (Fig. 5A). At this time the body was moving on average at a velocity of  $0.5 \pm 0.03 \text{ m s}^{-1}$  ( $N=35$ ), but in the best jumps a velocity of  $0.9 \text{ m s}^{-1}$  was achieved. The acceleration was applied over an average period of 14.9 ms (see above) giving a value of  $36 \text{ m s}^{-2}$ , or in the best jumps  $75 \text{ m s}^{-2}$  equivalent to  $8 g$  (Table 1). *Timema* expended  $19 \mu\text{J}$  of energy to achieve its best jumps generating a power output of  $1.6 \text{ mW}$  and exerting a force of  $3.6 \text{ mN}$ .

To estimate whether the extensor tibiae muscles of the hind legs can meet the requirements for jumping the following measurements were made. The tendon of the extensor tibiae muscle is 1.5 mm

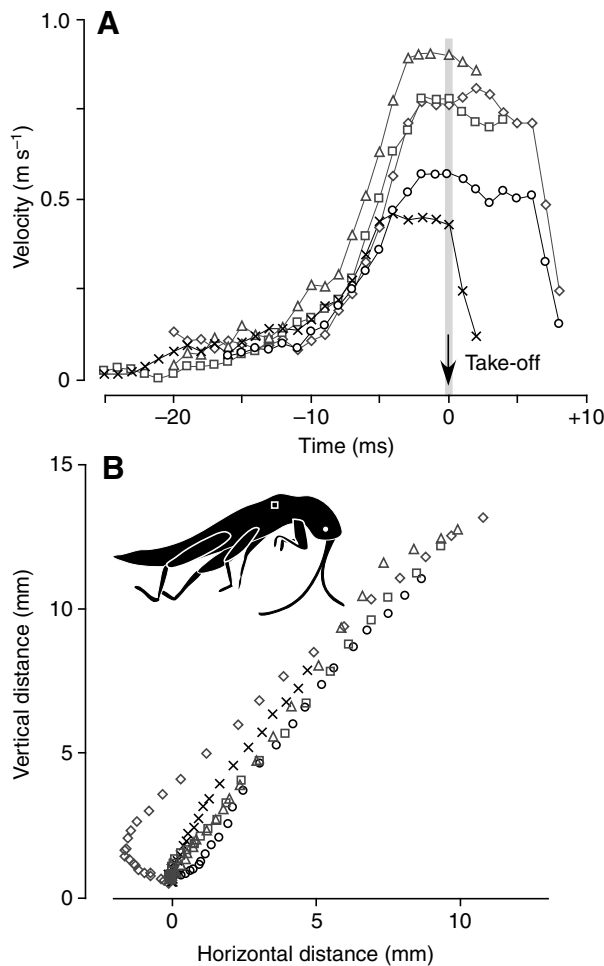


Fig. 5. Velocity and trajectory of five jumps by two *Timema*. (A) Peak velocity plotted as three point rolling average against time. The maximum velocity of the body is reached at  $-2$  ms before take-off. (B) Trajectories of the jump normalised for the same starting point and direction. The open square on the cartoon shows the point on the thorax that was measured for these graphs.

long and  $150\text{ }\mu\text{m}$  wide and the muscle fibres arise from both sides of it at angles that range from  $10\text{--}40^\circ$ , with many at  $25^\circ$  (taken as the mean pinnation angle). Both sides of the tendon have a total area of  $0.45\text{ mm}^2$  so that the physiological cross sectional area of the extensor tibiae muscle, given by the product of the tendon area and the sine of twice the pinnation angle (Callow and Alexander, 1973), is  $0.34\text{ mm}^2$ .

The ground reaction forces measured from the high speed images (average  $1.7\text{ mN}$  to maximum of  $3.6\text{ mN}$ ) would require a force of

$13.6$  to  $28.8\text{ mN}$  in each of the two leg muscles if they operated with a moment arm ratio of  $16$  (see above). This would need a muscle stress of  $40\text{ mN mm}^{-2}$  to produce an average jump and a stress of  $85\text{ mN mm}^{-2}$  to produce the best jumps. The extensor tibiae muscle of a locust is predicted to have stresses as high as  $750\text{ mN mm}^{-2}$  during jumping (Bennet-Clark, 1975) so the much lower estimates for *Timema* suggest that its extensor tibiae muscles could readily generate the forces required for a jump.

The trajectories of forward jumps were also calculated from the movements of the same part of the thorax as used to calculate velocity. The angle of the body relative to the ground was typically low ( $34.9 \pm 2.5^\circ$ ,  $N=33$ , range  $5\text{--}60^\circ$ ) and the mean take-off angle was  $38.9 \pm 2.46^\circ$  ( $N=33$ , range  $11\text{--}86^\circ$ ). Five of the 35 jumps performed at right angles to the camera are shown in Fig. 5B. In some jumps there was an initial backwards movement of the body that preceded the tibial extension movements of the hind legs, but even in these jumps a similar trajectory was followed once the movements of the hind legs began.

The forward trajectory of a jump typically took *Timema* to a height equivalent to a few body lengths and to a distance of  $80\text{ mm}$ , though some jumps achieved less (Fig. 6). Once airborne, the abdomen was progressively curled forwards so that its tip was at right angles to the more anterior abdominal segments. The antennae were pointed downwards so that they were the first to contact the ground during the descent phase of a jump. The orientation of the body remained stable throughout the jump and it did not rotate about either its transverse or longitudinal axes.

A backwards jump could be generated in response to an object approaching from the front. A similar sequence of movements propelled these jumps, but a key difference was always in the initial positioning of the hind legs (Fig. 7). At the start of the jump shown, the hind femora and tibiae were held almost parallel to the abdomen and to the ground and thus did not project dorsally above the dorsal surface of the abdomen. As the hind legs began to extend from this position, the abdomen was also curled further forwards. At take-off the hind legs were fully extended and were pointed downwards and slightly forward to the thorax, the head and antennae were also pointed downwards, but the tip of the abdomen pointed directly upwards. The thrust of the hind legs therefore propelled the body both upwards and slightly backwards in a trajectory that reached its apogee some  $40\text{ ms}$  after take-off. The backwards descent took the insect to a feet first landing about  $1.5$  body lengths from its starting position.

The initial position of the hind legs in a backward jump could be below the horizontal so that upon extension of the tibiae they generated a thrust that was directed backwards (Fig. 8). As a consequence, instead of the tip of the abdomen being lifted from the ground, it moved downwards after take-off, and once in contact with the ground acted as a pivot about which the rest of the body was rotated backwards. *Timema* then performed a

Table 1. Jumping performance of *Timema chumash*

	Time to take-off (ms)	Take-off velocity ( $\text{m s}^{-1}$ )	Mass (mg)	Length (mm)	Acceleration ( $\text{m s}^{-2}$ )	$g$ force	Energy ( $\mu\text{J}$ )	Power (mW)	Force (mN)
Formulae					$f=v/t$	$g=f/9.86$	$e=0.5 Mv^2$	$=e/t$	$=Mf$
Average	$14.9 \pm 0.28$ ( $N=46$ )	$0.53 \pm 0.02$ ( $N=43$ )	$47.5 \pm 7.3$ ( $N=6$ )	$12.0 \pm 0.68$ ( $N=6$ )	36	4	7	0.5	1.7
Best	12	0.9			75	8	19	1.6	3.6

Calculations of acceleration ( $f$ ),  $g$  force, energy ( $e$ ), power and force according to the formulae given are based on the measurements given in the preceding columns.

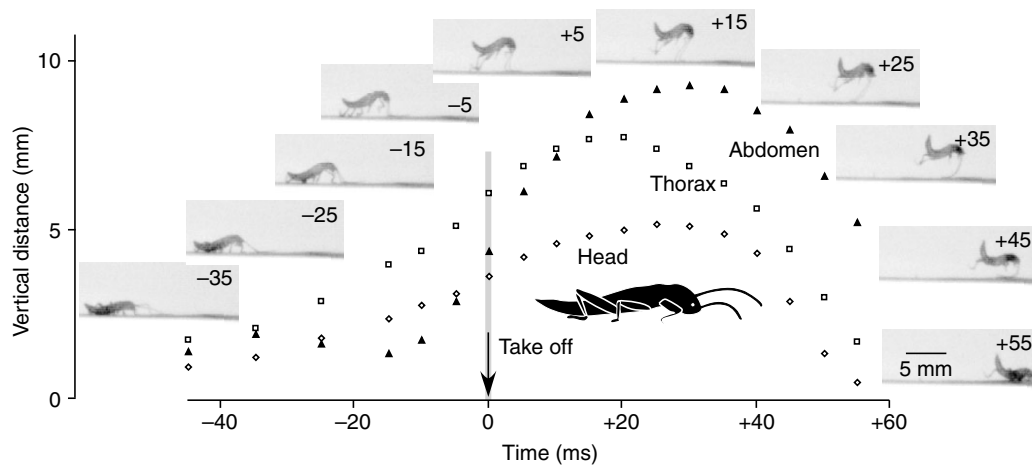


Fig. 6. Complete trajectory of a forward jump. The position of three points on the body are plotted [front of the head (diamonds), tip of the abdomen (triangles) and the same position on the thorax as in Fig. 5 (squares)]. Selected frames from the sequence are shown at the times indicated. The cartoon in this and subsequent figures shows *Timema* at the start of the jump to emphasise the position of the hind legs.

backwards summersault landing head first and upside down. The net effect was nevertheless to displace the body rapidly backwards and thus away from a potential predator approaching from the front.

#### DISCUSSION

*Timema* can propel its body rapidly forwards or backwards by jumping. These movements are powered by the simultaneous extension of the tibiae of the hind legs from fully flexed positions about the femora. The extension movements of these legs take 12 ms in the best jumps propelling the body to heights of some 20 mm and distances up to 80 mm at take-off velocities of  $0.9 \text{ m s}^{-1}$ . Many jumps, however, achieve smaller heights and distances, and lower take-off velocities. An object approaching from behind elicits a forward jump and one approaching from in front a backward jump, suggesting that they represent adaptive escape movements.

#### Body shape for jumping

The body of *Timema* is flattened dorsoventrally and is cryptically coloured. A contrasting feature with other stick insects is that all the legs emerge ventrally from the thorax so that their coxae are not visible when viewed dorsally. The hind legs are 1.5 times the length of the front legs so that they are proportionately longer than the hind legs of other stick insects such as *Carausius* which do not jump (Table 2). Compared with *Sipyloidea*, the only stick insect described that jumps (Burrows and Morris, 2002), the hind legs are again proportionately longer. Nevertheless, the hind legs are only about half the length of the body, placing *Timema* alongside those jumping insects that also have proportionately short hind legs relative to body length. This group includes froghoppers, in which the hind legs are 1.5 times the length of the front legs and 66% of the body length (Burrows, 2006a). A second group of insects has hind legs that are long, both relative to the other legs and the length of the body, and includes insects such as locusts with hind legs 2.7 times

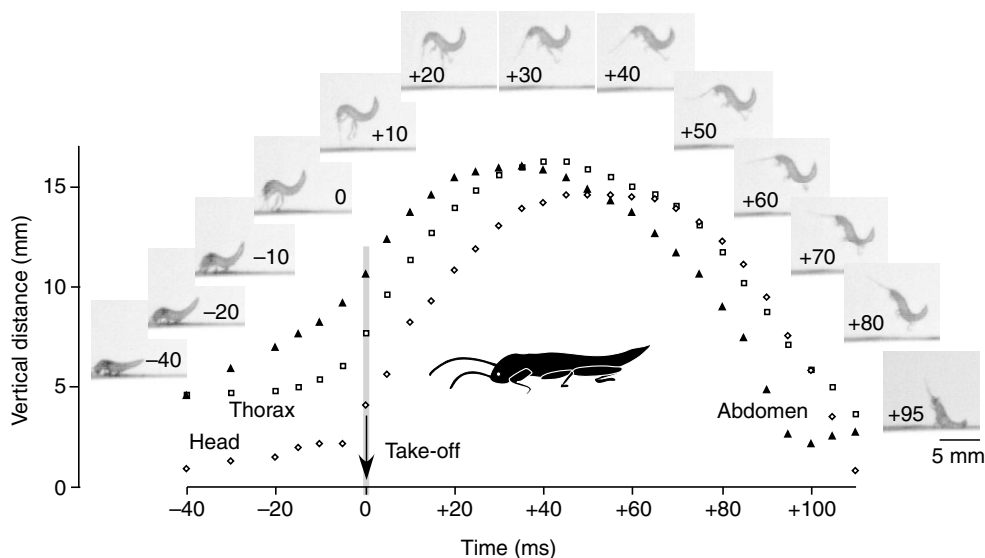


Fig. 7. Trajectory of a backwards jump. The same points on the body are plotted as in Fig. 6.

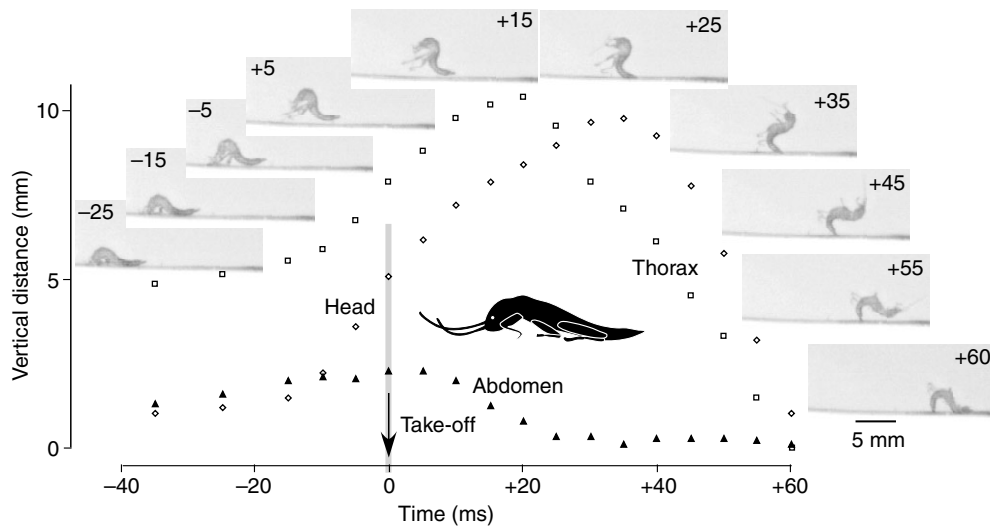


Fig. 8. Complete trajectory of a backwards somersault. The head initially points to the left. The thrust of the hind legs pushes the tip of the abdomen downwards to contact the ground and then forces the body backwards about this pivot point. The insect finishes with its dorsal surface on the ground and its head pointing toward the right.

the length of the front legs and as long as the body, and bush crickets with hind legs that are three times the length of the front legs and almost twice the length of the body (Burrows and Morris, 2003). Fleas and leafhoppers are intermediate, with hind legs twice the length of the front legs and 80% of body length. The short-legged jumpers use a catapult mechanism whereas bush crickets with very long hind legs rely on the leverage that such legs provide.

### Jumping performance

How does the jumping performance of *Timema* compare with that of other jumping insects? *Timema* reaches similar take-off velocities but accelerates faster than males of the stick insect *Sipylloidea*, which takes 100 ms to accelerate its 0.164 g body to a take-off velocity

of 0.6–0.8 m s<sup>-1</sup> (Burrows and Morris, 2002). The take-off velocity also comes close to matching that of fleas but the acceleration time is longer (Bennet-Clark and Lucey, 1967; Rothschild et al., 1972). *Timema* also achieves comparable take-off velocities to some of the larger European flea beetles, which also propel their jumping by extension of the hind tibiae (Brackenbury and Wang, 1995).

The performance, however, falls well short of that achieved by locusts (Bennet-Clark, 1975), bush crickets (Burrows and Morris, 2003), froghoppers (Burrows, 2003; Burrows, 2006a) and leafhoppers (Burrows, 2007b), which achieve much higher take-off velocities and exert more force relative to body mass. Froghoppers, for example, accelerate their 0.012 g body in less than 1 ms to take-off velocities of some 4.7 m s<sup>-1</sup> (Burrows, 2003; Burrows, 2006a). A male bush

Table 2. Comparison of body shape in stick insects, and in other jumping insects

	Best take-off velocity (m s <sup>-1</sup> )	Mass (g)	Body length (mm)	Ratios of leg lengths			Hind legs as % body length
				Front	Middle	Hind	
<i>Timema chumash</i> (female; N=6)	0.9	0.048±0.03	12±0.03	1	1	1.5	57±3
<i>Sipylloidea</i> sp Thailand 8 <sup>1</sup> (male; N=10)	0.6	0.16±0.004	65±0.05	1	0.7	1	64±0.03
<i>Carausius morosus</i> * (female; N=10)	Does not jump	1.1±0.03	78±0.03	1	0.8	0.9	39±0.03
Bush cricket, <i>Pholidoptera griseoaptera</i> <sup>2</sup> (female; N=7)	2.1	0.6±0.04	23±0.08	1	1.1	3	158±0.03
False stick insect <i>Prosarthritis teretirostris</i> <sup>3</sup> (male; N=8)	2.5	0.28±0.01	68±0.8	1	1.1	2.2	78±0.06
Locust, <i>Schistocerca gregaria</i> <sup>4</sup> * (female gregarious; N=7)	3.2	1.8±0.14	66±1.0	1	1.2	2.7	103±1.9
Flea beetle <i>Altica lythris</i> <sup>5</sup> * (N=10)	0.75±0.04	0.012±0.0006	4.9±0.1	1	1.1	1.4	78±2.1
Flea <i>Spilopsyllus cuniculus</i> <sup>6</sup> *	1.0	0.00045	1.5	1	1.3	1.9	57
Froghopper <i>Philaenus spumarius</i> <sup>7</sup> (N=7)	4.7	0.012±0.007	6.1±0.08	1	1	1.5	66±1.4
Leafhopper <i>Cicadella viridis</i> <sup>8</sup> (female; N=7)	1.6	0.019±0.0011	9.2±0.033	1	1	1.9	82±2.03
<i>Hackeriella veitchi</i> <sup>9</sup> (N=10)	1.5	0.0014±0.00003	3±0.03	1	1	1	65±1.5

<sup>1</sup>Data from (Burrows and Morris, 2002).

<sup>2</sup>Data from (Burrows and Morris, 2003).

<sup>3</sup>Data from (Burrows and Wolf, 2002).

<sup>4</sup>Velocity from (Bennet-Clark, 1975).

<sup>5</sup>Velocity (average), mass and body length from (Brackenbury and Wang, 1995).

<sup>6</sup>Velocity and mass from (Bennet-Clark and Lucey, 1967).

<sup>7</sup>Data from (Burrows, 2006a; Burrows, 2006b).

<sup>8</sup>Data from (Burrows, 2007a; Burrows, 2007b).

<sup>9</sup>data from (Burrows et al., 2007).

\*Other data from Burrows (unpublished).

Data are from males and females unless gender is specified. Mass, body length, and hind legs as % of body mass, are given as means and s.e.m.



cricket (Pholidoptera) takes 30 ms to accelerate its 0.42 g body to  $1.5 \text{ m s}^{-1}$  with females achieving a take-off velocity of  $2.1 \text{ m s}^{-1}$ . The forces generated by the extensor tibiae muscles during jumping appear to be well within the capabilities of ordinary striated muscles. The muscle mass that *Timema* devotes to propelling jumping is only 0.6% of total body mass and is therefore much lower than the 12% devoted by froghoppers (Burrows, 2007c) and the 6% by locusts (Bennet-Clark, 1975). The power requirements of *Timema* for jumping appear, however, to be higher than could be generated by direct muscle contraction, implying that the extensor tibiae muscles of the hind legs should contract slowly in advance of the jump being released and store the energy they generate in some skeletal or muscular structures. The exact mechanisms of energy storage and release requires recordings from muscles to determine the pattern of their motor spikes and hence their time course of activation. Do the extensor and flexor tibiae muscles co-contract as in the locust, or are there mechanical restraining devices as in froghoppers? It also requires a detailed analysis of where the energy might be stored.

The femora of *Timema* are much stouter than those of the front and middle legs with the maximum width some 75% greater, but there are few other specialisations of the hind legs which would appear to aid jumping. The femoro-tibial joint has no semi-lunar processes, as in grasshoppers and locusts, which could act as devices for storing the energy generated by the contractions of the extensor tibiae muscles. Energy might be stored at other sites such as the femoral cuticle or the tendon of the extensor tibiae muscle. Even in locusts that have prominent semi-lunar processes only half the energy for jumping is stored in them, with the other half stored in other structures (Bennet-Clark, 1975).

### Biology of the jump

What is the purpose of the jumping in *Timema*? By adjusting the initial positions of the hind legs the movement can be directed either forwards or backwards and away from a potential threat. Nevertheless, the relatively short distances that are moved by *Timema* in both the vertical or horizontal direction suggest that escape is from a small potential predator or parasite. The short distances travelled would enable *Timema* to fall rapidly from the branch on which it was perching. Such a movement would take them out of the visual field of larger predators such as birds and thus place less reliance on the rapidity of the movement itself and more on the camouflage qualities of its body in the new but not very distant position. The lack of wings implies that jumping must serve purposes other than launching into flight.

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