# Effectiveness and efficiency of two distinct mechanisms for take-off in a derbid planthopper insect

By

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With 8 Figures and 2 Tables: 3 movies as Supplementary Material

Keywords: locomotion, jumping, high speed imaging, escape movements

Running Title: Two take-off mechanisms in a derbid planthopper

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# ABSTRACT

Analysis of the kinematics of take-off in the planthopper *Proutista moesta* (Hemiptera, Fulgoroidea, family Derbidae) from high speed videos showed that individual insects used two distinct mechanisms involving different appendages. The first was a fast take-off (55.7% of 106 take-offs by 11 insects) propelled by a synchronised movement of the two hind legs and without participation of the wings. The body was accelerated in 1 ms or less to a mean take-off velocity of 1.7 m s-1 while experiencing average forces of more than 150 times gravity. The power required from the leg muscles implicated a power-amplification mechanism. Such take-offs propelled the insect along its trajectory a mean distance of 7.9 mm in the first 5 ms after take-off. The second and slower take-off mechanism (44.3% of take-offs) was powered by beating movements of the wings alone with no discernible contribution from the hind legs. The resulting mean acceleration time was 16 times slower at 17.3 ms, the mean final velocity was six times lower at 0.27 m s-1, the ***g*** forces experienced were 80 times lower and the distance moved in 5 ms after take-off was 7 times shorter. The power requirements could be readily met by direct muscle contraction. The results suggest a testable hypothesis that the two mechanisms serve distinct behavioural actions; the fast take-offs could enable escape from predators; the slow take-offs that exert much lower ground reaction forces could enable take-off from more flexible substrates while also displacing the insect in a slower and more controllable trajectory.

# INTRODUCTION

Launching from a surface into the air is accomplished in the majority of adult insects by two sets of propulsive appendages, the legs and the wings. Wingless adult insects and many larvae have to rely on the legs alone, although in, for example, springtails (Brackenbury and Hunt, 1993; Christian, 1978; Christian, 1979), trap jaw ants (Gronenberg, 1995; Patek et al., 2006) and click beetles (Evans, 1972; Evans, 1973; Kaschek, 1984) different parts of the body are used. Take-off has to meet many different demands; at one extreme, rapidity of action is required to escape from stimuli that indicate a potential predator with little time for feedback adjustments; at the other extreme are requirements to launch into flight with a controllable trajectory through dense vegetation. In between may be the need to move to a nearby leaf for more food, or to locate a mate. This paper analyses an insect which uses two distinct jumping mechanisms to overcome these disparate demands; first, a rapid take-off propelled solely by the hind legs and second, a much slower mechanism powered by entirely by repeated movements of the wings. It asks what advantages these different mechanisms might confer?

A catapult mechanism in the hind legs is used by many of the most accomplished insects for taking-off rapidly, such as locusts (Bennet-Clark, 1975), froghoppers (Burrows, 2006), planthoppers (Burrows, 2009), fleas (Bennet-Clark and Lucey, 1967; Rothschild et al., 1975; Rothschild et al., 1972; Sutton and Burrows, 2011), and flea beetles (Brackenbury and Wang, 1995; Nadein and Betz, 2016). Bush crickets also use their hind legs to jump but use direct contractions of their muscles instead of a catapult mechanism (Burrows and Morris, 2003). Other insects may use the direct contraction of muscles in two pairs of legs to propel take-off and some may then combine leg propulsion with wing movements. For example, wingless ants (Tautz et al., 1994) propel take-off by movements of both the middle and hind pairs of legs. Lacewings (Neuroptera) start to move their wings only when the insect is fully airborne as propelled by the legs (Burrows and Dorosenko, 2014). Caddis flies (Trichoptera) propel take-off by movements of the middle and hind legs, either with or without a contribution from flapping movements of the wings (Burrows and Dorosenko, 2015b).

In butterflies (Lepidoptera) analysis of the movements of the wings at take-off (Sunada et al., 1993) indicates that they alone cannot generate sufficient force to achieve take-off (Bimbard et al., 2013), thus implicating a contribution from the legs. In small moths take-off is propelled by movements of the middle and hind legs while the wings remained closed (Burrows and Dorosenko, 2015a). In increasingly heavier species of moths, beating of the wings is more likely to accompany the leg movements and precede take-off. In treehoppers (Hemiptera, Membracidae) the rapid movements of the hind legs that alone can propel take-off may also be accompanied by beating movements of the wings (Burrows, 2013b).

The fly *Drosophila melanogaster* has two take-off strategies but both involve propulsion by the middle legs combined with wings movements (Card and Dickinson, 2008; Hammond and O'Shea, 2007; Trimarchi and Schneiderman, 1995). In so-called voluntary take-offs (now called “long mode” (von Reyn et al., 2017)), an initial wing elevation occurs before the legs start to move that results in a slower and more stable trajectory once airborne (Card and Dickinson, 2008). In visually evoked escape (“short mode”), the wings are folded over the body and substantially more power is delivered by middle leg movements resulting in faster velocities but instability once airborne (Card and Dickinson, 2008); stability is traded against speed in these two strategies.

Mosquitoes, *Anopheles coluzzi*, face the problem that their body mass can double after a blood meal so that forces must increase to effect a take-off preferably without arousing the attention of the host (Muijres et al., 2017). This is achieved by increasing the stroke amplitude of the wing to generate more of the necessary force relative to that generated by the legs which would be transmitted to the skin of the host. Their long legs also keep ground reaction forces below the threshold that the host can detect by distributing them over a longer time. Similarly, the dolichopodid fly *Hydrophorus alboflorens* can take-off from the surface of water by flapping its wings without the legs exerting force on the surface (Burrows, 2013a). If the same wing movements are then combined with movements of the middle and hind legs then the take-off time is substantially reduced and the take-off velocity increased. This speed advantage is offset against the danger that the propulsive legs could penetrate the water surface and consequently trap the insect.

In the preceding examples a combination of different mechanisms are used; legs alone can propel take-off or they can be combined with movements of the wings. Here we analyse a species of derbid planthopper that has one fast and one slow take-off strategy and show that each is produced by a different mechanism involving different appendages. The fast movement is propelled by the rapid movements of the hind legs without any contribution from the wings. By contrast, the slow movement is generated by repetitive, beating movements of the wings without any propulsive movements of the legs. The same individual insect can use both mechanisms interchangeably. We analyse the very different take-off performances produced by these two mechanisms, assess their relative efficiencies and discuss the possible behavioural uses to which they are put.

# MATERIALS AND METHODS

Adults of *Proutista moesta* (Westwood, 1851) were collected in September and October 2017 from sugar cane (*Saccharum* *officinarium* Linnaeus) and *Agave* sp. in the grounds of the University of Agricultural Sciences (Gandhi Krishi Vigyan Kendra), Bangalore, Karnataka State, India. These planthoppers belong to the order Hemiptera, super family Fulgoroidea and family Derbidae and are considered as possible vectors of Kerala wilt disease of coconut palms (Edwin and Mohankumar, 2007; Ramachandran Nair, 2002). Photographs of live insects were taken with a Nikon D7200 camera fitted with a 105 mm Nikon lens. The morphology of the legs was examined in live insects, and in those fixed in 70% alcohol. Leg and body lengths were measured to an accuracy of 0.1 mm from images captured on a Nikon SMZ 25 microscope with a Nikon DS-Ri2 camera (Nikon Instruments, Melville, NY, USA) and projected onto a large monitor screen. Body masses were determined to an accuracy of 0.1 mg with a BSA224S-CW (Sartorius) balance (Sartorius Lab Instruments, Goettingen, Germany).

Sequential images of take-off were captured at a rate of 5000 s-1 and an exposure time of 0.1 ms, with either a Phantom v611 or Phantom v1212 high speed camera (Vision Research, Inc., Wayne, N.J., U.S.A.) fitted with a 105 mm Nikon lens. Images from the camera were saved directly to a computer for later analysis. The insects were free to move in a chamber with an internal width of 32 mm, height of 25 mm and depth of 12 mm. The front wall was made of optical quality glass; the floor, side walls and ceiling were constructed from 12 mm thick, closed cell foam (Plastazote, Watkins and Doncaster, Cranbrook, Kent, UK). Preliminary observations indicated that take-offs were of two types; first with a fast take-off velocity and second those with a much slower take-off velocity. Take-offs of both types occurred spontaneously and without any overt mechanical stimulus; just one fast take-off was elicited by a touch to the tip of a front wing with a fine paint brush. Both types of take-off could also occur from any surface, but only those from the floor were analysed so that the effects of gravity were the same for all take-offs. The camera pointed at the centre of the chamber, the shape of which meant that most take-offs were in the image plane of the camera. Those that deviated to either side of this plane by ± 30o were calculated to result in a maximum error of 10% in the measurements of joint or body angles. Tracks of the movements of particular body parts were made manually frame by frame with Tracker software (http://physlets.org/tracker/); auto-tracking was not used. The frame at which a particular leg lost contact with the ground was determined by playing the video backwards and forwards frame by frame. An abrupt shift in position of a tarsus indicated that it was no longer load bearing and had therefore lost contact with the ground. Take-off was indicated when the last leg lost contact with the ground and was designated as time t = 0 ms. The acceleration time for take-off was defined as the period from the first detectable, propulsive movement of the legs, or of the propulsive movement of the wings, until take-off. Peak velocity was calculated as the distance moved in a rolling 3 point average of successive images before take-off. A point on the body that could be recognized in successive frames and was close to the centre of mass was selected for measurements of the trajectory. The angle subtended by a line joining these points after take-off, relative to the natural horizontal, gave the trajectory angle. The body angle at take-off was defined as the angle subtended by the longitudinal axis of the insect relative to the natural horizontal. The results are based on the analysis of high speed videos of 106 take-offs by 11 insects at a temperature of 25º C. At least three jumps were analysed in detail for each individual. Measurements are given as means ± standard error of the mean (s.e.m.) for an individual and as mean of means (grand means) for a particular take-off strategy by all insects.

# RESULTS

## Shape of body and legs

*P. moesta* had a mean mass of 2.02 ± 0.88 mg (N=13 insects) and a mean body length of 2.5 ± 0.03 mm (N= 8 insects). Both males and females were included together as no sex differences were found in the values for these two measures of body form. The insects could be readily recognised on the leaves of their host plants by the black and white markings on the upper surface of the long front wings and by the postures of the wings that were adopted (Fig. 1). The most commonly observed resting posture was for the wings to be raised above the body and pointed both laterally and backwards. The wings thus subtended a mean angle 27.1 ± 1.2 degrees to the vertical midline axis as viewed from in front (Fig. 1A), and a mean angle of 88.1 ± 1.1 degrees (N=10 insects) to the longitudinal axis of the body, as viewed from the side (Fig. 1B). A less commonly observed posture was for the wings to be folded over the back of the insect (Fig. 1D). The front wings were 6.14 ± 0.09 mm long (N=8) and thus more than twice the length of the body so that they projected almost 4 mm beyond the tip of the abdomen when folded (Fig. 1D). The hind wings, by contrast, were much shorter at 3.2 ± 0.06 mm, N=8) so that when moved in flight they fitted the space behind the shaped trailing edge of the front wings.

The parts of all three pairs of legs were thin and of similar diameter with none showing swollen regions that could accommodate a greater volume of muscle (Fig. 1C). Only the hind tibiae had spines and these were restricted to the ventral surface at the articulation with the tarsi. The lengths of the legs had a ratio relative to the front legs of: 1 front: 0.96 middle: 1.15 hind (Table 1). The longer hind legs were 106% of body length compared with 92% for the front legs and 88% for the middle legs. The length of the femora of all the legs were not statistically significantly different (paired samples *t*-test for comparison of middle and hind legs, *t*8 =0.658, *P* =0.529, N=8). The increased length of the hind legs was instead due to their tibiae which were 27% longer than the middle tibiae (paired samples *t*-test for comparison of middle and hind tibiae, *t*8 =9.246, *P* = 2 ×10-5, N=8).

## Kinematics of take-off movements

In the 106 take-offs by 11 insects that were analysed, 59 (55.7%) were propelled by a synchronised movement of the two hind legs that was not accompanied by wing beating and resulted in a fast take-off velocity. The remaining 47 (44.3%) take-offs were propelled by beating movements of the wings with no observable propulsive movements of the legs. The net result was a take-off with a much slower velocity. Of the 11 insects analysed, three did not perform analysable fast take-offs and one did not perform any analysable slow take-offs. The overlapping data sets for the following analysis thus consisted of 8 insects performing 59 fast take-offs and 10 insects performing 47 slow take-offs. The same insect could thus produce both types of take-off during a recording period and either type could occur spontaneously (without any observable inducing stimulus). For example, a fast take-off could be followed directly by another fast take-off, or by a slower one so that there was no apparent pattern to the sequence of take-off movements of one insect and no indication that fatigue or habituation might favour the use of one type over the other. To test whether the performance of a particular type of jump influenced the next jump, the proportions of fast jumps that were followed directly by another fast jump were compared to the overall occurrence of fast and slow jumps. 68% of fast jumps were followed by another fast jump, whereas fast jumps represented only 58% of the total take-offs that occurred (Chi-square = 3.775, with one degree of freedom, *P* = 0.052). It follows therefore that a slow jump was less likely to be followed by another slow jump. All take-offs were recorded in the same chamber under the same lighting and temperature conditions so that each individual insect experienced the same sensory environment. High speed videos were initially divided into separate sets on the basis of the speed of take-off. The separation into fast and slow take-offs was subsequently supported by differences in the kinematics and by a comparison of the measurements of different parameters of the take-off performance.

## Fast take-off

In preparation for a fast take-off, the trochantera of both hind legs were always fully levated about their respective coxae and the wings started from their raised position pointing backwards and laterally over the body as viewed from the side (Fig. 2) and behind (Fig. 3). The full levation of the hind legs was most clearly seen in frames -1.2 ms and -1 ms of a rear view of the insect (Fig. 3). The hind legs were the first to move when both hind trochantera began to be depressed about their respective coxae. This movement marked the beginning of the short (mean of means 1.05 ± 0.05 ms, N=8 insects (Table 2)) acceleration phase of take-off. In the videos (Figs. 1, 2 and Movies 1 and 2 Supplementary Material) this was seen as a movement of the femur relative to the body because the trochanter and femur moved together. In the few remaining frames leading to take-off, the coxo-trochanteral joints of the hind legs continued to depress progressively and the femoro-tibial joints to extend progressively so that the hind legs straightened (Figs 2, 3). This movement was in turn associated with an upwards and forwards displacement of the body. The front and middle legs did not show any consistent changes in their joint angles that indicated a contribution toward movement of the body(Fig. 3). These legs also lost contact with the ground between 0.4 - 0.2 ms before take-off, so could not contribute propulsive force to the latter part of the acceleration phase. Only when the body was raised sufficiently so that the front and middle legs were no longer load-bearing was there a change in their joint angles. The progressive changes in the angle of a hind femur relative to the body and of the hind tibia relative to the femur, seen clearly in a rear view, contrasted with the absence of changes in these angles in the middle legs and front legs (see stick diagrams of the legs in Fig. 3). Synchronous and progressive movements of the two hind legs were particularly apparent in a view from behind (Fig. 3). At take-off the hind legs were almost fully outstretched and the distal tips of their tarsi were the last to lose contact with the ground. This marked the end of the acceleration phase of take-off and that the insect was now airborne.

The interrelations of the movements of the legs, wings and body were tracked during take-off and their positions plotted in the *x* and *y* axes (Fig. 4A) and the *y* axis movements were also plotted against time (Fig. 4B). The first movements of hind legs began 1 ms before take-off, as indicated by the downward movement of the hind femoro-tibial joint and their effects were reflected first in the movements of the body and head and then of the front tarsus as it lost contact with the ground (Fig. 4A,B). The wings started to fold at an initial rate of 30 degrees ms‑1, 0.5 ms after the hind legs first began their depression and extension movements and 0.5 ms before take-off, but they did not reach their fully folded position until after 3 ms after take-off (Figs 2 and 4B).

These fast take-offs were thus propelled by a single, synchronised movement of the two hind legs with any contribution from the wings limited to a possible reduction of drag as they were folded over the body.

## Slow take-off

A slow take-off also started with the wings raised above the body but although the hind legs were levated they were not consistently moved into their most fully levated position (Fig. 5, Movie 3 Supplementary Material). The first movement in preparation for take-off was now a twisting of the wings rather than a depression movement of the hind legs as in the preceding fast take-offs. In this particular example, the wing movements started 17 ms before take-off (Figs 5 and 6A-C). After completing this first twisting movement, the wings moved back to their original position and then executed a complete depression movement in which they were swept downwards and forwards in front of the head. Sometimes their tips brushed against the ground but did not apply a force that propelled the insect upwards or forwards. This was followed by a full elevation taking the wings above and behind the head. During the next cycle of depression all the legs lost contact with the ground so that take-off occurred (Fig. 6A,B). The acceleration time to take-off (17 ms in this example) thus encompassed an initial small amplitude cycle of wing twisting, followed by one and half cycles of full amplitude wing beating. The complexity and timing of events leading to take-off was revealed by plotting the position of the head, body, a front wing and a hind leg in the *x* and *y* axes (Fig. 6A), against time (Fig. 6B, C).

Each cycle of wing movements was associated with a distinct displacement of the head and body (Fig. 6C). By contrast, during these wing movements, the coxo-trochanteral and femoro-tibial joint angles of the legs did not change in a way which might have indicated that they were applying forces to the ground which would contribute to lifting the body. The hind and middle legs remained stationary through most of the acceleration phase, but sometimes showed a small movement about the coxo-trochanteral and femoro-tibial joint angles approximately 5 ms after the first movements of the wings and again a few milliseconds before take-off. Only the joint angle of the front legs appeared in some take-offs to change because they became straighter as the angle of the body relative to the ground increased from 17 degrees at the start of the acceleration phase to 41 degrees at the end. A small sag of the legs could be seen in some insects as the front, middle and hind legs progressively lost contact with the ground. There was a positive correlation between wing movements and the forward and upward movements of the whole insect (Fig. 6C) but there was no similar correlation with leg movements. After take-off, the wings continued to beat with a cycle period of 10 ms so that there was a smooth transition to powered flight. A comparison of slow and fast take-offs that occurred sequentially in the same insect, highlighted the large differences in the leg movements between the two mechanisms (Fig. 7A,B). In a fast take-off, the coxo-trochanteral and femoro-tibial joints in the hind legs underwent large angular changes progressively associated with body movements leading to take-off (Fig. 7A). By contrast, in a slow take-off the angular changes of these joints of the hind legs were 3.5 times smaller and the front and middle legs showed no changes that were consistent with providing propulsion (Fig. 7B). Slow take-offs were thus propelled by flapping movements of wings with little discernible contribution from movements of the legs.

## Take-off performance

Key parameters of take-off performance were markedly different for the fast and slow mechanisms of take-off and were thus dependent upon whether the hind legs or the wings generated the propulsive force (Table 2).

### Acceleration time

When take-off was propelled by the hind legs, the acceleration time was rapid and was completed in 1.05 ± 0.05 ms (mean of means, N = 8 insects and 59 take-offs) compared with a much slower time of 17.3 ± 1.93 ms (mean of means, N = 10 insects and 47 take-offs) when take-off was propelled by the wings. These acceleration times for the two take-off mechanisms are significantly different (*t*-test: t16 = 7.49, *P* = 1×10‑5) with the values forming two non-overlapping data sets. In the best take-offs (defined as reaching the highest take-off velocity), the acceleration times when using the legs for propulsion could be reduced to as little as 0.6 ms whereas the shortest time when using the wings was 12.6 ms.

### Take-off velocity

The mean take-off velocity was also higher at 1.74 ± 0.20 m s‑1 (mean of means, N = 8 insects) when propulsion was generated by the hind legs compared with 0.27 ± 0.01 m s-1 when wings generated the propulsion. There is a significant difference in these non-overlapping values (*t*-test: t16 = 8.19, *P* = 4.1×10-7). In the best jumps propelled by the hind legs velocities could reach as high as 3.6 m s-1 whereas the best take-off velocities when propelled by the wings could only reach 0.4 m s-1.

### Body angle at take-off

The mean of means angle of the body relative to the ground at take-off was much shallower at 25.95 ± 3.63 degrees in the same group of insects when propelled by the legs compared with 55.56 ± 2.26 degrees when propelled by the wings. These values are again statistically significantly different (*t*-test: t12 =4.62, *P* = 1×10-3).

### Trajectory

The two different mechanisms for launching take-off did not, however, result in angles of trajectory that were significantly different (mean of means 62.61 ± 6.04 degrees for fast take-offs compared with 67.23 ± 7.03 degrees, *t*-test: t14 = 0.41, *P* = 0.69) for slow ones propelled by the wings.

### Acceleration

The short acceleration times and high velocities of fast take-offs resulted in an insect experiencing accelerations of a mean of 1657 m s-2 rising to a maximum recorded value of 6033 m s-2 in the best (= fastest) take-offs. In slow take-offs the mean acceleration was only 16 m s-2 rising to a maximum value of 32 m s-2. These differences were also reflected in forces of as high as 615 ***g*** being experienced in fast take-offs compared with just 3 ***g*** in slow ones.

### Energy, Power and Force

The same method was used to calculate the energy (E, in Joules) expended in propelling the body from the ground into the air, for both slow and fast take-offs.

E= 0.5 *m* v2

Where *m* = mass, kg

v = velocity, m s-1

In a fast take-off generated by a single rapid movement of both hind legs a mean of 3.1 μJ were expended in raising the body, more than 30 times higher than the mean of 0.1 μJ in a slow take-off. The force applied was also larger in fast as opposed to slow take-offs (Table 2). The power requirements were again different.

### Distance moved in 5 ms after take-off

A behaviourally relevant measure of the outcome of these two take-off mechanisms was the distance that an insect moved in a defined period after take-off and before the drag effect of wind resistance started to curtain performance (Vogel, 2005). In fast take-offs the insect was propelled a mean distance of 7.9 ± 1.07 mm in 5 ms after take-off or 7 times further than the 1.10 ± 0.06 mm achieved after a slow take-off (Fig. 8). These values describe non-overlapping sets that are significantly different from each other (*t*-test: t16 = 7.138, *P* = 2×10-7). No significant differences in the distance moved for different trajectory angles were found for either the fast or slow take-off mechanisms (Fig. 8).

# DISCUSSION

Individuals of the same species of a derbid planthopper use two distinct mechanisms to generate two quite different types of take-off. These two mechanisms of propulsion were used interchangeably by the same individuals and the resulting performances form two non-overlapping sets of data. Fast take-offs were propelled by a rapid and synchronous movement of the two hind legs only and slow take-offs were propelled by beating of the wings alone. Fast take-offs as compared with slow take-offs had an acceleration time that was 16 times shorter, a take-off velocity that was 6 times faster, a force applied to the ground that was 100 times greater, resulting in the insect being propelled 7 times further in the first 5 ms after take-off. In fast take-offs the mean value of the power output was nearly 700 times greater than in slow take-offs.

## Fast take-offs are propelled by a catapult mechanism

Assuming the leg muscles responsible for the rapid movements of the hind legs in fast take-offs represent 10% of body mass, then in the best take-offs the power requirement of approximately one hundred thousand W kg-1 (Table 2) is more than 200 times the capability of normal muscle (Askew and Marsh, 2002; Ellington, 1985; Josephson, 1993; Weis-Fogh and Alexander, 1977). This implies that power amplification would be needed. In another family of planthoppers (Issidae) (Burrows and Bräunig, 2010) and in froghoppers (family Cercopidae) (Burrows, 2007) large paired trochanteral depressor muscles in the thorax contract slowly in advance of a jump and thereby mechanically distort specific parts of the metathoracic internal skeleton (Burrows et al., 2008). The energy stored in these structures is then released suddenly to power the rapid movements of the hind legs. Insects using this mechanism are capable of jumping with shorter acceleration times and faster take-off velocities than insects which rely on direct contractions of muscles to power a take-off (see Table 3 in (Burrows and Dorosenko, 2017a)). This mechanism requires specialisations of the power-generating muscles, of the skeleton to allow distortions that store energy while allowing body shape to recover in time for the next take-off, of mechanisms that release the stored energy and of the nervous system to generate the complex motor patterns that underlie these rapid movements. By contrast slow take-offs require few, if any, adaptations of structures that fulfil other locomotor functions.

## Slow take-offs are propelled by wing movements

The power needed to generate the slow take-offs is low (a mean value of 21 W kg-1 rising only to 63 W kg-1 in the best take-offs) and well within the capacity of direct contractions of muscles. Take-off is achieved by beating the wings without any measurable contribution from the legs; the small angular changes that occur in the leg joints do not occur in a consistent pattern that indicates a contribution to the thrust that would raise the body from the ground. In addition, there is likely to be a slight alteration in aerodynamic forces generated by the flapping wings when the insects are in close proximity to the ground.

## Energy efficiency

Which of the two distinct mechanisms used for take-off is the most energy efficient? To seek an answer to this question, the same calculations based on the kinematics were used for both mechanisms. In fast take-offs propelled by the hind legs a mean of 3.1 µJ were involved in transmitting force to the ground through the legs, but that in slow take-offs propelled by wing beating the energy fell by 31 times to just 0.1 µJ (Table 2). Moreover, during slow take-offs, only 21 W kg-1 of power were observed to accelerate the insect from the ground. Assuming that the flight muscles have a power capacity 100-300 W kg-1 (Ellington, 1985), approximately 7-20% of the muscle power available is being used to generate motion, with the rest (80-93%) being lost to viscous wind forces, moving the wings and accelerating the air beneath the wings. In contrast, during a fast take-off powered by the hind legs, less than 5% of its energy is lost to wind-drag (Bennet-Clark and Alder, 1979), less than 2% to moving the legs (Sutton and Burrows, 2010) and no energy is lost to moving air beneath the wings. On these measures, in fast take-offs powered by the hind legs more energy is put into propelling the insect from the ground than in slow take-offs powered by the wings where energy is lost to generating the repetitive movements of the wings and in moving the air leaving only a small amount that could be used to move the body up. In the wasp *Pteromalus puparum* that propels take-off by the direct contractions of muscles in its middle and hind legs without the need for a catapult mechanisms, this form of take-off is also more energetically efficient than that of other wasps of similar mass that use wing beating to generate take-off (Burrows and Dorosenko, 2017b).

## Why two mechanisms for take-off?

The derbid, *P. moesta* has a catapult mechanism for generating take-offs with a short acceleration time and a fast take-off velocity and that is energetically more efficient than jumps propelled by wing movements. Why then should it have a second mechanism that has a much longer acceleration time, a much slower take-off velocity and that is energetically less efficient? Moreover, because separate muscles and appendages are used – fast take-off requires the catapult action of hind leg muscles whereas slow-take-off requires repetitive contractions of muscles moving the wings – then decisions to select one mechanism rather than the other must feed into distinct and separate motor pathways. These different mechanisms suggest a testable hypothesis that fast and slow take-offs serve very different behavioural demands. Fast take-offs meet all the likely demands of a rapid escape from, for example, the gaze of a predatory bird or the attention of a parasitoid wasp. Any instability in the resulting trajectory due to rotation of the body would add further unpredictability that the predator would have to track. Even an uncontrolled landing would be a better outcome than the fate that would otherwise result. Slow take-offs could be used for more controlled movements from compliant surfaces to adjacent leaves for food, or to meet a potential mate. Two observations support this suggestion. First, propelling take-off by wing movements reduces the ground reaction forces compared to those exerted by the hind legs in fast take-offs, that should enable take-off from more compliant leaves without losing energy to distortion of the substrate (Burrows and Sutton, 2008). Second, these insects spend much of their time feeding on the underside of leaves. Take-off may thus require little propulsive force when aided by gravity and the wing beating can lead to precise navigation through vegetation and a slow, measured landing on nearby food sources.

# ACKNOWLEDGEMENTS

M.B is particularly grateful to all the students in Bangalore who helped with this work and whose enthusiasm and engagement were so infectious as to drive the project forwards. We thank our Cambridge and Bangalore colleagues for their comments on the manuscript.

# COMPETING INTERESTS

No competing interests declared.

# FUNDING

M.B. received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors. S.S. was supported by a grant from the Air Force Office of Scientific Research, USA.

# AUTHOR CONTRIBUTIONS

M.B. initiated the project. H.M.Y collected the insects. M.B. and A.G. carried out the experimental work. M.B. and M.D. analysed the videos to determine take-off performance. M.B. constructed the figures and wrote the first draft of the paper. A.G., H.M.Y., S.S. and M.D. contributed to subsequent versions.

# FIGURE LEGENDS

## Fig. 1

**Body form of *P. moesta* as related to take-off.** (A) Photograph of a front view with the front wings raised above the body. (B) Smaller side view with the wings raised. The pink lines in (A, B) define the angle of the wings relative to the longitudinal body axis. (C) Photograph of a front, middle and hind leg. (D) Side view with the wings folded over the body. In this and Figures 2, 3 and 5, the left front (LF) and right front (RF) legs are indicated by arrows with yellow heads, the left middle (LM) and right middle (RM) legs by arrows with white heads, and the left hind (LH) and right hind (RH) legs by arrows with pink heads.

## Fig. 2

**Fast take-off by *P. moesta* from the horizontal propelled by the hind legs and viewed from the side.** Images were captured at 5000 s-1 and with an exposure time of 0.1 ms and are arranged in two columns with the timing of the frames given relative to take-off at time = 0 ms. The hind legs began to move at -1 ms. The wings began to be folded onto the body at take-off and this process continued for a few milliseconds when airborne. The triangles in the bottom left hand corners of each image are a constant, spatial reference point here and in Figs 3 and 5.

## Fig. 3

**Fast take-off by from the horizontal *P. moesta* propelled by the hind legsand viewed from behind.** Images were captured at 5000 s-1 and with an exposure time of 0.1 ms and are arranged in three columns. Take-off occurred 1 ms after the first movements of the hind legs. The wings were open initially and then were folded gradually but did not beat.

## Fig. 4

**Tracks of body parts during a fast take-off powered by the hind legs.** Images of this take-off are shown in Figure 2. (A) The distances moved in the *y*-axis are plotted against those in the *x*-axis for the tip of the right wing (cyan circles), the head (green diamonds), the right front tarsus (yellow circles) and the right hind tarsus (pink triangles). The black arrows show the position of the different body parts against the frame at take-off and the arrows with white heads the subsequent positions at +3 ms after take-off. (B) The distances moved in the *y*-axis are plotted against time (ms). The position of the femoro-tibial (FT) joint (pink circles) of the right hind leg is also included. Take-off is completed in 1 ms. The same symbols for body parts as here are also used in Figs 6 and 7.

## Fig. 5

**Slow take-off by *P. moesta* from the horizontal propelled by the wings.** Images were captured at 5000 s-1 and with an exposure time of 0.1 ms and are arranged in three columns. The wings started to move at -17 ms and were in the process of completing the second depression phase at take-off. They continued to beat after take-off giving a smooth transition to powered, flapping flight.

## Fig. 6

**Tracks of body parts during a slow take-off powered by the wings.** Images of this take-off are shown in Figure 5. (A) The distances moved in the *y*-axis are plotted against those moved in the *x*-axis for the head, the tip of the right front wing, front tarsus and hind tarsus. The black arrows indicate positions at take-off; the orange arrows and arrow heads indicate the direction of movement of the tip of the right front wing. (B) The distances moved in the *y*-axis by the same body parts are plotted against time (ms). It takes 17 ms to accelerate in this slow take-off compared with 1 ms in a fast take-off. (C)Each cycle of wing movement is accompanied by a forward displacement of the head and body.

## Fig. 7

**Comparison of legs movements during fast and slow take-offs.** Two successive take-offs by the same individual using the two different mechanisms are shown. **(**A) A fast take-off powered by the hind legs. Changes in the hind leg angles between the trochanter and coxa (measured as changes in the angle of the femur about the body) and the femur and tibia started 1 ms before take-off. In the hind leg, the body/femur went through an angular change of 120 degreesand the femoro-tibial joint changed by 140degreesbefore take-off. By contrast the same joints of the other two pairs of legs changed little, with the only marked change occurring in the front legs when they lost contact with the ground. (B) A slow take-off powered by the wings. Only small changes in the joint angles of all the legs were associated with the body lifting slowly from the ground.

## Fig. 8

**Differences in the effectiveness of the two mechanisms for take-off.** The distances (mm) that the insect was propelled along its trajectory was measured 5 ms after take-off and plotted against trajectory angles; open circles for fast take-offs propelled by rapid movements of the hind legs, filled squares for slow take-offs propelled by wing movements. Ninety seven take-offs by 11 insects are plotted. The regression lines for both fast and slow take-offs show no significant differences from a horizontal line indicating no dependence of distance covered on trajectory angle.

# SUPPLEMENTARY MATERIAL

## Movie 1

Fast take-off propelled by movements of the hind legs of *P. moesta* viewed from the side, captured at 5000 frames s-1 and with an exposure time of 0.1 ms and replayed at 10 frames s-1. See main text Fig. 2.

## Movie 2

Fast take-off propelled by movements of the hind legs of *P. moesta* viewed from behind, captured at 5000 frames s-1 and with an exposure time of 0.1 ms and replayed at 10 frames s-1. See main text Fig. 4.

## Movie 3

Slow take-off propelled by movements of the wings of *P. moesta* viewed from the side, captured at 5000 frames s-1 and with an exposure time of 0.1 ms and replayed at 10 frames s-1. See main text Fig. 6.

**Table 1. Body form of *Proutista moesta***

Body length and mass, and lengths of the front and hind femora and tibiae. N indicates the number of individuals from which the measurements were taken; males and females are combined. The ratio of leg lengths is given relative to the front legs.

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **Body Mass, mg** | **Body Length, mm** | **Front leg, Femur, mm** | **Front leg, Tibia,**  **mm** | **Hind leg, Femur, mm** | **Hind leg, Tibia,**  **mm** |  | **Ratio of leg lengths** |  | **Hind leg length as % of body length** | **Hind leg length (mm)/ body mass ^ 1/3 (mg)** |
|  |  |  |  |  |  |  | **Front** | **Middle** | **Hind** |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
| *P. moesta* (N=8) | 2.02 ± 0.9 (N=13) | 2.5 ± 0.03 | 0.77 ± 0.01 | 1.04 ± 0.02 | 0.67 ± 0.02 | 1.37 ± 0.02 | 1 | 0.96 | 1.15 | 106 | 2.17 |
|  |  |  |  |  |  |  |  |  |  |  |  |

**Table 2. Jumping performance of *Proutista moesta*.**

Comparison of take-off performance using two mechanisms: 1. **Fast take-off propelled by hind legs** . 2. **Slow take-off propelled by wings** . Data in columns 2–6 are the grand means (± s.e.m.) for the measured jumping performance of all insects analysed. The values in columns 7–12 are calculated from these means. N = number of individuals performing this type of take-off. The best performance is based on the take-off with the highest velocity.

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **Body Mass** | **Time to take- off** | **Take-off velocity** | **Take-off angle** | **Body angle at take-off** | **Acceleration** | **g force** | **Energy** | **Power** | **Force** | **Power/kg muscle** |
| **Formula** | ***m*** | **t** | **v** |  |  | **f= v/t** | ***g*= f/9.81** | **E=0.5 *m* v2** | **=E/t** | **=*m* f** | **=power / (.1*m*)** |
| **Units** | **mg** | **ms** | **m s-1** | **degrees** | **degrees** | **m s-2** | ***g*** | **µJ** | **mW** | **mN** | **W kg−1** |
| **1. Fast take-off propelled by hind legs** |  |  |  |  |  |  |  |  |  |  |  |
| Average (N=8) | 2.0 ± 0.1 | 1.05 ± 0.05 | 1.7 ± 0.2 | 62.6 ± 6.04 | 26.0 ± 3.6 | 1657 | 169 | 3.1 | 2.9 | 3.4 | 14417 |
| Best | 2.3 | 0.6 | 3.6 | 42.0 | -12.0 | 6033 | 615 | 15.1 | 25.1 | 13.9 | 109203 |
|  |  |  |  |  |  |  |  |  |  |  |  |
| **2. Slow take-off propelled by wings** |  |  |  |  |  |  |  |  |  |  |  |
| Average (N=10) | 2.0 ± 0.1 | 17.3 ± 1.9 | 0.27 ± 0.01 | 67.2 ± 7.0 | 55.6 ± 2.3 | 16 | 2 | 0.1 | 0.004 | 0.03 | 21 |
| Best | 2.0 | 12.6 | 0.40 | 87.0 | 47.0 | 32 | 3 | 0.2 | 0.01 | 0.06 | 63 |
|  |  |  |  |  |  |  |  |  |  |  |  |

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